Evolutionary theory of human warfare: genes, individuals, groups

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To my parents,

To Canmore,

& To Rebecca,

who knows why.

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> *Se noi non vediamo in una scienza uno dei tanti rami della sapienza, allora questa scienza ci sembra priva d'interesse, fredda, arida lontana dall'uomo. Se in ogni scienza noi vediamo un ramo dell'albero della sapienza allora ogni scienza ci appare in tutto il suo significato.*
>
> If in every discipline we do not see one of the many branches of the tree of wisdom, this discipline will appear devoid of interest, cold, far from man. If in every discipline we see a branch of the tree of wisdom, then every discipline will appear to us in all its meaning[1].

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[1] De Giorgi, E. 2002. Valore sapienzale della matematica. In: G. Tanzella Nitti and A. Strumia, eds. Dizionario interdisciplinare di Scienza e Fede. Rome: Urbaniana University Press. pp. 841–848. Translation my own

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I, Alberto Jacopo Cesare Micheletti, do hereby certify that this thesis, submitted for the degree of PhD, which is approximately 59,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for any degree.

I was admitted as a research student at the University of St Andrews in September 2015.

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Publications

The following published papers have arisen from this thesis:

- ◊ Micheletti, A. J. C., Ruxton, G. D. and Gardner, A., 2017. Intrafamily and intragenomic conflicts in human warfare. *Proc. R. Soc. B*, 284, 20162699.

- ◊ Micheletti, A. J. C., Ruxton, G. D. and Gardner, A., 2018. Why war is a man’s game. *Proc. R. Soc. B*, 285, 20180975.

Both are my own work, supervised by Andy Gardner and Graeme Ruxton.

Abstract

Recent years have seen an explosion of multidisciplinary interest in coalitionary intergroup aggression – i.e. warfare – in human societies, and considerable advances in our understanding of its origins and evolutionary-ecological drivers. However, the study of human warfare has largely neglected the possibility that different parties – e.g. men versus women, younger versus older generations, or attacking versus defending groups – might have different incentives to influence the expression of warfare-related behaviours, which may result in conflicts of interest within and between groups and sex differences in behaviour. In this thesis, I develop a mathematical evolutionary framework, based on kin-selection theory, to investigate such differences in incentives, with special attention to sex-specific demography as a potential driver of conflicts of interest at multiple levels of the biological organisation. I find that: (a) the ecology of warfare can drive the evolution of sex-biased dispersal, which in turn modulates intrafamily and intragenomic conflicts over warfare-related behaviours, with the latter leading to parent-of-origin-specific gene expression (genomic imprinting) and maladaptive behavioural disorders; (b) almost-exclusively male warfare can be driven by an evolutionary feedback between male and female participation in battle, rather than fundamental differences between the sexes; (c) sex is a fundamental modulator of altruism in the context of the demography of warfare, with the sex that competes more globally and/or is more philopatric being favoured to behave more altruistically towards same-sex groupmates than opposite-sex ones; (d) conflicts of interest within and between attacking and defending groups inhibit the formation of military alliances and the shift to large-scale human societies more generally. Taken together, these results suggest that differences in incentives for different parties in the context of warfare – often driven by sex-biases in demographic parameters – result in behavioural sex differences and conflicts of interest within and between different organisational levels.

Contents

1 Introduction

兵者	War is A grave affair of state
國之大事	It is a place
死生之地	Of life and death A road
存亡之道	To survival and extinction
不可不察也	A matter To be pondered carefully

– Sun Tzu, *The Art of War*
(trans. John Minford)

The puzzle of human warfare

Warfare – that is, coalitionary intergroup aggression, in its broadest definition (Wrangham, 1999; Choi and Bowles, 2007; Bowles, 2009; Lehmann and Feldman, 2008; Wrangham and Glowacki, 2012) – has been a nearly universal feature of human societies throughout time and sadly continues to be so in the contemporary world (Gat, 2006; Glowacki, et al., 2017), notwithstanding suggestions that the frequency of armed hostilities and the rates of death from such events have declined in the past few centuries (Pinker, 2011). The possible origins and drivers of warfare have been explored by intellectuals worldwide for millennia, with the first formalisations being developed by philosophers in ancient Greece and China (Keeley, 1997; Gat 2006; Sun Tzu, 5th century BC (2009); Glowacki, et al., 2017). The rise of evolutionary theory – with the publication of *The Origin of Species* (Darwin, 1856) and *The Descent of Man* (Darwin, 1871) – started a revolution in our understanding of warfare: coalitionary intergroup aggression was, for the first time, conceptualised as an evolved human behaviour that might have emerged through the action of natural selection (Glowacki, et al., 2017).

However, this insight did not result in a productive research programme in the decades following Darwin. Cultural anthropology, which was born in the 1870s with the goal of studying the origins of human society and cultural diversity, at first employed the idea of evolution as a loose framework that accommodated ladder-like views of social change, and in later years often downplayed – or utterly rejected – biological explanations of human behaviour (Bowler, 2009; Glowacki, et al, 2017). For example, influential American anthropologist Margaret Mead (1940) argued that war was a cultural invention, rather than a biological adaptation. This view became dominant in anthropology, especially in the United States (Glowacki, et al., 2017).

Later, in the 1960s, a number of 'colloquial science' publications, aimed at both experts and members of the general public, challenged this idea (Milam, 2019). These books – the most influential being *On aggression* (Lorenz, 1963 (1966)), *The Territorial Imperative* (Ardrey, 1966), and *The Naked Ape* (Morris, 1967) (but see also *Men in Groups* (Tiger, 1969) and *The Imperial Animal* (Tiger and Fox, 1971)) – presented some of the latest studies in ethology and other disciplines, and applying their conclusions to humans, argued that aggression and warfare in our own species had deep biological roots (Laland and Brown, 2011; Milam, 2019). At the same time, they expounded the thesis that the very advanced capacities for aggression and organised warfare that characterised humans were at the basis of our species' uniqueness and were the key drivers of human social evolution – a view that came to be known as 'killer ape' theory (Milam, 2019). While enjoying considerable success with the general public, these works were then criticised by professional scientists for adopting group adaptationist thinking (e.g. Alexander and Tinkle, 1968), and for their simplifications and often naïve applications of ethological results to human behaviour (e.g. Alexander and Tinkle, 1968; Wilson, 1975)

The 'killer ape' theory finally fell out of favour in the 1970s, as researchers in academic institutions were reacting against it in favour of a more balanced view (Milan, 2019). At the same time, observations by Jane Goodall and colleagues that intergroup killing occurred in chimpanzees (Goodall, et al., 1979) led to the rejection of human exceptionalism (Milam, 2019). A rigorous evolutionary study of warfare – and human behaviour in general – finally began to develop in the late 1960s and then in the 1970s, when key emerging theories in evolutionary biology, including kin selection theory, the maximisation of an individual's inclusive fitness (Hamilton, 1964) and the gene's eye view of evolution (Williams, 1966; Dawkins 1976) were imported by a new generation of anthropologists into their discipline (Glowacki et al., 2017).

The first attempts to such a synthesis were developed by Alexander and Tinkle (1968), who suggested a verbal argument for how warfare-related behaviours could be favoured by individual-level selection, and by Durham (1976), who suggested that intergroup aggression could be seen as an adaptation, at least in some cases, and reviewed warfare in small-scale human societies (Tooby and Cosmides, 1988). Both suggested that human intergroup aggression could have deep evolutionary roots, but gave equal importance to cooperation (unlike supporters of 'killer ape' theory) and recognised roles for both biology and culture (Alexander and Tinkle, 1968; Durham, 1975). Later, Tooby and Cosmides (1988) approached the question of the evolution of human warfare from an evolutionary psychology perspective, offering the first speculations on the role of a ‘coalitionary psychology’ in human intergroup conflict.

These first cross-disciplinary interactions led, in the following decades, to the contemporary evolutionary anthropological study of human warfare, which has blossomed in recent years with a flurry of studies in high-profile publications (Glowacki, et al., 2017). The field is also benefitting from contributions from other disciplines – psychology (van Vugt, 2009), history (Gat, 2006; Morris, 2014), political science and international relations (Johnson and Toft, 2014; Lopez, 2016) – and is increasingly multi- and inter-disciplinary. Crucially, these efforts have clarified that warfare is influenced both by genetic factors and by environmental effects of various nature, including culture (Glowacki, et al., 2017). While loci underpinning intergroup violence specifically (rather than violence in general) have not been identified to my knowledge, aggression is a trait with substantial heritability: roughly half of the variance is explained by genes, while the other half is explained by environmental factors, in both men and women (estimated from meta-analyses of twin and adoption studies; Tuvbald and Baker, 2011). There is some evidence suggesting that a number of neurotransmitter pathways (serotonin, dopamine, norepinephrine, GABA) are involved in the modulation of aggression, with mutations in the genes underlying them (e.g. monoamine oxidase A gene (*MAOA*), serotonin transporter gene (*SLC6A4*)) resulting in aggression disorders (Yanowich and Coccaro, 2011; Anholt and Mackay, 2012). It is important to underline that aggression in humans and other animals is controlled by multiple loci, with epistatic and pleiotropic effects playing an important role (Anholt and

Mackay, 2012). Systems genetics studies in non-human model species, such as mice and fruit flies, promise to shed light on the genetic architecture of aggression (Anholt and Mackay, 2012).

The evolutionary study of warfare has developed and continues to develop along four main research avenues (Gat 2006; Glowacki, et al., 2017). The first seeks to investigate the evolutionary roots of warfare by studying intergroup conflict in non-human animals, employing the comparative method (Glowacki, et al., 2017). Efforts have focused on chimpanzees, our closest living relatives and the only other primate that routinely engages in lethal intergroup conflict, with groups of males entering a neighbouring territory and killing isolated males (though intraspecific coalitionary killing has been reported in spider monkeys and mountain gorillas; Manson and Wrangham, 1991; Wrangham 1999; Wrangham and Glowacki, 2012; Glowacki, et al., 2017). This work has underlined the importance of resources and mates as ultimate drivers of intergroup violence and suggested that escalation to killing is much more likely to occur when one side far outnumbers the other ('imbalance of power' hypothesis; Manson and Wrangham, 1991; Wrangham, 1999).

The second research avenue consists in the archaeological study of material evidence of warfare in prehistoric humans, in the form of mass graves and skeletal remains with signs of physical trauma and violent death (Glowacki, et al., 2017). Numerous such archaeological discoveries relating to pre-agricultural societies (e.g. Holocene, hunter-gatherers; Mirazón-Lahr, et al., 2016) and groups with simple, subsistence agriculture (e.g. Neolithic farmers in Europe; Teschler-Nicola, 2012; Wahl and Trautmann, 2012; Meyer, et al., 2015) have been made and analysed in recent years. This work adds to the evidence that war has deep roots and was already present before the establishment of complex agriculture

(Keeley, 1996), further dispelling the myth that intergroup violence was absent in prehistoric peoples (the 'myth of the peaceful savage' that prevailed before the 1960s-70s; Glowacki, et al., 2017).

The third avenue aims to expand our knowledge of the origins and drivers of warfare by studying contemporary hunter-gatherer groups (Gat, 2006; Bowles, 2009; Wrangham and Glowacki, 2012; Glowacki, et al., 2017) and other small-scale societies, that is horticulturalists, pastoralists or subsistence agriculturists characterised by the absence of political officials (Wrangham and Glowacki, 2012; Glowacki, et al., 2017). It is assumed that human populations survived by hunting and gathering for most of our species' history, that is from the Pleistocene to the emergence of agriculture in the Early Holocene (Foley, 1995; Marlowe, 2005; Gat, 2006; Bowles, 2009). For this reason, contemporary hunter-gatherers – whose societies generally number in the hundreds or thousands and are subdivided into residential groups or 'bands' of 25-40 people (Wrangham and Glowacki, 2012) – are considered the best models to understand Pleistocene humans' ecology and behaviour (Foley, 1995; Marlowe, 2005; Gat, 2006; Bowles, 2009). However, caution is warranted as contemporary hunter-gatherers are likely to have more complex technology than prehistoric humans, might have in some cases been influenced by contact with agricultural societies, and might reside in environments that are not representative of the ones inhabited by Pleistocene humans (Marlowe, 2005). Other small-scale, non-hunter-gatherer, societies – whose groups can number in the hundreds or even thousands – are also considered by some to be valuable systems to study the evolution of coalitionary intergroup aggression (Wrangham and Glowacki, 2012; Glowacki, et al., 2017). This is because, like hunter-gatherers, they practice 'simple warfare' or 'warfare below the military horizon', that is raiding and feuding in the absence of political or military hierarchies (Wrangham and Glowacki, 2012; Glowacki, et al., 2017). Again, caution should be exercised when trying to generalise results obtained in the study of these societies, as their economies differ substantially from those likely to have characterised Pleistocene humans.

Several reviews of intergroup behaviour in hunter-gatherers and other small-scale societies (Ember, 1978; Boehm, 1999, Otterbein, 2004; Gat, 2006; van der Dennen, 2007; Wrangham and Glowacki, 2012) have revealed that warfare is present in the majority of these populations, even though the frequency and intensity of conflicts varied with ecological/social factors and peaceful interactions are possible. With regard to hunter-gatherers, Wrangham and Glowacki (2012) identify several parallels between hunter-gatherer and chimpanzee warfare (e.g. surprise ambushes, increased reproductive success for victorious males), but also highlight significant differences, most notably the use of weapons, leading to higher risks for aggressors – and complex strategising (see also Glowacki, et al., 2017).

Finally, the fourth avenue centres on the use of various forms of mathematical modelling – to test the logical correctness of existing hypotheses, provide proofs of concept and generate new predictions (Servedio, et al., 2014) – and has provided stimulating insights into human warfare in very recent years (Glowacki, et al., 2017). For example, in a much-discussed study, Choi and Bowles (2007) explored the possibility that warfare might have coevolved with altruistic behaviours towards the ingroup, and thus may help explain the high levels of cooperation observed in human societies – a connection originally suggested by Darwin (1871) and later analysed by Hamilton (1975). The study, which included both game-theoretic and agent-based modelling components, showed that altruism and parochialism (i.e. hostility towards members of other groups) could have evolved together in early human societies, even with relatively low levels of war-related mortality (Choi and Bowles, 2007; see also Bowles, 2006, 2009).

Another key model of warfare was developed shortly afterwards by Lehmann and Feldman (2008), who employed the kin selection framework. They showed that altruistic behaviours in the context of war ('belligerence' and 'bravery') could evolve in a population subdivided into groups engaging in warfare, even with considerable group sizes (Lehmann and Feldman, 2008). In more recent years, other models have focused on exploring alternative ways for resolving the collective action problem surrounding participation in warfare – that is, the fact that single individuals benefit from participation of their groupmates but, paying a cost when participating themselves, they are incentivised to "free-ride", reducing their efforts (e.g. Gavrilets and Fortunato, 2014). Yet others have started to formalise mathematically long-standing suggestions that war has had a key role in the evolution of complex human societies, through alliance, conquest or subordination (Turchin and Gavrilets, 2009; Gavrilets, et al., 2010; Turchin, 2010; Turchin, et al., 2013).

Aims and structure of the thesis

As illustrated in the previous section, recent years have seen great advances in our understanding of the origins and drivers of human warfare. However, the possibility that different parties – e.g. men and women, members of younger and older generations, or of attacking and defending groups – might have different incentives with regards to the expression of war-related behaviours has been relatively neglected. Paradoxically, the study of intergroup violence in human groups has largely failed to explore how such differing incentives might become manifested in conflicts of interest within and between groups, and sex differences in behaviour. Furthermore, the possible role of demography – i.e. population group structure and the movement of individual between patches – and especially of sex biases in migration rates has not been considered. The potential for asymmetries in incentives, conflicts of interest and behavioural differences in the context of war – such as those described above – deserves both theoretical and empirical exploration.

In this thesis, I develop theoretical contributions to the broad theme identified immediately above by exploring a number of questions within it. The general aim and motivation of the thesis is to employ evolutionary theory methods to start illuminating differences in incentives between parties at multiple levels of the biological organisation – genes, individuals, groups – their possible manifestations in conflicts of interest and/or behavioural sex differences, and the role of demography in mediating these. To tackle these questions – which are detailed in the next paragraph – I develop mathematical models of warfare, based on kin selection theory (Hamilton, 1964). Specifically, I reformulate a model originally developed by Lehmann and Feldman (2008; Box1.1) and I expand it and adapt it to specific questions in each chapter. I adopt the same modelling framework – rather than developing an ad-hoc model for each chapter and question – to allow comparison between the chapters and with existing literature, exploring emerging themes and insights of the thesis in the general discussion (Ch.6).

It is important to underline that the primary goal of this thesis is not to develop predictive models parametrised to describe the biology of any specific human population at any specific time. Rather, it is to generate abstract, general models that illuminate the selective pressures surrounding warfare-related behaviours, and thus allow exploration of the logical plausibility of suggestions in the literature and the identification potential drivers of asymmetries in incentives between different parties (for more on the use of abstraction in evolutionary biological modelling, see Servedio, et al., 2014). In this spirit, I adopt a broad definition of warfare as ‘coalitionary intergroup aggression’ (Wrangham, 1999; Choi and Bowles, 2007; Bowles, 2009; Lehmann and Feldman, 2008; Wrangham and Glowacki, 2012) (Box 1.2), rather than one specifically tailored to a given human society (see Box 1.2 for details). Moreover, I model genetically-controlled behaviours and discuss potential interactions with cultural factors in the discussions to each chapter and in the general discussion. I present four research chapters, each tackling specific and well-defined questions within the broad theme of incentive asymmetries in warfare. Each chapter contains their own self-contained introduction and discussion.

In Chapter 2, I expand Lehmann and Feldman’s (2008) kin-selection model of warfare to: a) investigate the selective pressure on male dispersal and female dispersal in the context of warfare, exploring the possibility that the ‘ecology/demography of warfare’ itself (i.e. the movement of individuals between groups resulting from victory and defeat in intergroup confrontations) may drive sex-biases in dispersal; b) investigate conflicts of interest within the family (between young adult male warriors, their fathers and their mothers) and within individuals (between maternal-origin genes and paternal-origin genes) over two altruistic warfare-related behaviours, belligerence and bravery.

In Chapter 3, I adapt the model developed in Chapter 2 to explore the logical plausibility of current explanations for the almost-exclusive participation of men in warfare until very recent times (which rely on sex differences between in effectiveness, personal costs, and migration; Manson and Wrangham, 1991; Low, 1993, 2015; Gat 2000a,b,c, van

Vugt, 2009) and uncover potentially more fundamental mechanisms which might generate this empirical pattern.

In Chapter 4, I further expand the model developed in Chapter 2-3 to investigate how demographic parameters, including those that are specific to the intergroup aggression (the ‘ecology/demography of warfare’) may influence patterns of sex-specific altruism, broadly defined as a behaviour that increases the receiver’s competitiveness for reproductive opportunities, while decreasing the altruist’s (Hamilton, 1964; this behaviour is distinct from belligerence and bravery explored in Ch.2). Specifically, I explore how differences in demographic parameters may drive differences in male-to-male, male-to-female, female-to-male, and female-to-female altruism.

In Chapter 5, I adapt the life cycle and models in Chapter 2-4 to investigate the selective pressures on military alliances between groups – one of the potential pathways towards the formation of larger polities from smaller human groups. In separate but related analyses, I explore possible conflicts of interest between groups and within groups, between individual interests and group interests.

Finally, in Chapter 6, I provide a general discussion for the results presented in the thesis. I explore how my analyses illuminate the broad theme of incentive differences between various parties in the context of war, establishing links between results presented in different chapters. I place these results and insights in the context of the relevant literature and suggest new avenues for future empirical and theoretical exploration.

In the remainder of the present Chapter, I briefly present existing approaches to the evolutionary study of human behaviour and I then introduce the framework on which my contributions are grounded – social evolutionary theory – with special attention to themes and open questions that feature in the later chapters.

Box 1.1 – Lehmann and Feldman's (2008) model and its extensions

In 'War and the evolution of belligerence and bravery', Lehmann and Feldman (2008) develop a population genetic, kin-selection model of war between 'small-scale, pre-state societies' (*ibid.*, p.2882) with the aim of exploring the selective pressures on two genetically-controlled traits, 'belligerence' and 'bravery'. Both traits are only exhibited by subadult males and they are controlled by their adult fathers (i.e. the phenotype of the son does not depend on his own genotype but on his father's). Belligerence is assumed to be a trait that increases the probability that the carrier's group initiates a war against another group. Bravery, on the other hand, is assumed to be a trait that increases the probability that the carrier's group wins an attack war or a defence war against another group. Both traits determine a fitness cost for the individual subadult males exhibiting them. As is standard in this kind of models, the authors adopt Wright's (1931) infinite-island model of dispersal, that is they consider an infinite population subdivided into an infinite number of groups with random migration connecting them.

At the beginning of the life cycle, in each group, N_f adult females and N_m adult males mate randomly, with each of the adult females producing a large number of juveniles of either sex. Juveniles grow to become subadults, which then have the opportunity to disperse to a randomly-selected group, males with probability m_m and females with probability m_f (N.B. the authors allow for sex-specific rates of dispersal, but do not explore the consequences of differences in the dispersal behaviour of males and females, instead assuming m_m=m_f=m; Lehmann and Feldman, 2008, p.2879). The war phase follows, with a group attacking another group with probability a (a function of belligerence) and the attacker winning the war with probability ω (a function of bravery). Individuals then compete within their sex for the N_m male breeding positions and N_f female breeding positions in each group. In groups that were not attacked and either did not attack or attacked and lost the war, only individuals from that group compete for breeding positions. In groups that were attacked and lost, conquered individuals compete with conquering individuals: on average, conquered males obtain s_m breeding positions and conquering males $(1 – s_m)$ breeding positions and, analogously, conquered females obtain s_f breeding positions and conquering females ($1 - s_f$) breeding positions. The partial (or complete) repopulation of defeated groups by conquering individuals constitutes the fitness benefit of belligerence and bravery.

The authors perform a kin selection analysis, employing the inclusive fitness approach (Hamilton, 1964, 1970, 1975; see *Kin selection* section below), and thus obtain conditions under which belligerence and bravery are favoured by selection. They show that both traits can evolve even in groups of large size, with bravery evolving at least twice as readily, all else being equal, because it increases the probability of success in two ways, during attack wars and during defence wars. In addition, they show that, while the two traits can evolve through direct benefits alone (assuming zero relatedness between individuals), they evolve more readily when individuals within a group are related to some degree, in which case belligerence and bravery are altruistic behaviours (*sensu* Hamilton, 1964, 1970). Moreover, they show that the selective pressure on a mutant allele for either trait becomes stronger with decreasing group size N (where N=N_m=N_f), decreasing migration rate m (as the relatedness between groupmates increases), and increasing fractions of breeding spots obtained by conquering individuals in conquering groups $1 - s_m$ and $1 - s_f$ (as the inclusive fitness benefits accrued by subadult males increase).

The model by Lehmann and Feldman (2008) was later extended by Lehmann (2011) to explore the evolution of belligerence and bravery under two alternative demographic scenarios following the victory of a group over another: a) ‘defeated group repopulation’ (DGR) as in Lehmann and Feldman (2008), and b) ‘victorious group size expansion’ (VGE) in which a winning group extracts resources from the defeated group, which allow it to temporarily increase its carrying capacity. For mathematical tractability and in discontinuity with Lehmann and Feldman (2008), the model assumes a haploid population with clonal reproduction. The study shows that the selective pressures on belligerence and bravery are greater when defeated groups are – at least partially – repopulated by individuals from the victorious group. This is because, under this scenario (DGR), the benefits of warfare are exported away from the focal group (to the defeated group), while in the alternative scenario (VGE), group augmentation results in an increase in kin competition, which determines an inclusive fitness cost.

In this thesis, I expand Lehmann and Feldman’s (2008) model in several ways. In Chapter 2: I reformulate the model using the neighbour-modulated fitness approach to kin selection analysis (Hamilton, 1964, 1970, 1975) employing the Taylor-Frank method (Taylor and Frank, 1996; Box 1.3); I allow for an individual subadult male’s belligerence or bravery phenotype to be controlled by different parties, specifically themselves, their father, their mother, their paternal-origin genes, their maternal-origin genes. I introduce a sex-specific mortality cost for dispersal and distinguish between 'dispersal' proper, that is the probability that an individual leaves their natal group, and 'migration', the probability that an individual leaves their natal group and successfully becomes a member of another group (see Ch.2 'Extended methods' for full details).

In Chapter 3: starting from the model in Lehmann and Feldman (2008) and in Chapter 2, I rename bravery 'male participation [in warfare]' and I introduce a second trait only expressed by subadult female and termed 'female participation [in warfare]'. I study the coevolution of these two traits. I do not consider the evolution of belligerence, and I vary the probability that a group attacks another one as a parameter (see Ch.3 'Extended methods' for full details).

In Chapter 4: starting from the model in Lehmann and Feldman (2008) and in Chapters 2-3, I introduce four sex-specific altruism traits, where 'altruism' is broadly defined as a behaviour which increases the competitiveness for reproductive opportunities of the receiver and decreases that of the altruist (Hamilton 1964). Specifically, I consider: male-to-male altruism, male-to-female altruism, female-to-male altruism, and female-to-female altruism. I do not consider the evolution of belligerence and bravery, and I vary the probability that a group attacks another one and the probability that the attacking group wins as parameters (see Ch.4 'Extended methods' for full details).

In Chapter 5: starting from the model in Lehmann and Feldman (2008) and in Chapters 2-4, I alter the life cycle to allow the formation of military alliances between groups, crucially maintaining the same fitness generating events of the previous models. In the first part of the analysis, I introduce a trait exhibited by individuals which increases the probability that the carrier's group forms an alliance with another group – and I analyse the selective pressures acting on this trait when it is controlled by different classes of individuals in different groups. In the second part of the analysis, I introduce a trait – which I name 'diplomacy' – exhibited by young adult males in groups that have won a war against another group. This trait increases the probability that the carrier's group forms an alliance with a group they have defeated, but it is costly for the carrier as it reduces the fraction of reproductive opportunities available to him the defeated group. I do not consider the evolution of belligerence and bravery, and I vary the probability that a group attacks another one and the probability that the attacking group wins as parameters (see Ch.5 'Extended methods' for full details).

Box 1.2 – Controversy over the definition of warfare and the definition adopted here

A considerable controversy over the definition of warfare has developed in the past decade, coinciding with a resurgence in interest in this topic in research across multiple disciplines and the publication of some studies in high-profile journals (e.g. Bowles, 2009; Fry and Söderberg, 2013).

A number of researchers, both empiricists (e.g. Wrangham, 1999; Wrangham and Glowacki, 2012) and theoreticians (e.g. Choi and Bowles, 2007; Lehmann and Feldman, 2008; Lehmann 2011), adopt a broad definition of warfare as 'events in which coalitions of members of a group seek to inflict bodily harm on one or more members of another group' (Bowles, 2009, p.1294) or, more concisely, 'coalitionary intergroup aggression'. This definition includes all instances in which a subset of more than one individual from a given group aggresses at least one individual from another group, and thus includes revenge killings perpetrated by an offended party and their associates and feuding (Bowles, 2009). It also includes all possible modalities of intergroup conflict, from surprise ambushes or raids (characteristic of hunter-gatherer societies and chimpanzees, for example) and pitched battles (more common between larger-scale societies) (Wrangham and Glowacki, 2012).

On the other hand, other researchers (Otterbein, 2004; Fry, 2007; Fry and Söderberg, 2013) adopt a definition that excludes revenge-motivated ambushes/raids and feuding. For example, Fry (2007, Ch.2) defines war as:

> A group activity, carried on by members of one community against members of another community, in which it is the primary purpose to inflict serious injury or death on multiple nonspecified members of that other community, or in which the primary purpose makes it highly likely that serious injury or death will be inflicted on multiple nonspecified members of that community in the accomplishment of that primary purpose.

In this thesis, I adopt the former (broader) definition (Wrangham, 1999; Choi and Bowles, 2007; Bowles, 2009; Lehmann and Feldman, 2008; Wrangham and Glowacki, 2012) for three reasons. Firstly, this is the definition adopted by Lehmann and Feldman (2008), whose model I reformulate and expand to address the questions posed in this thesis. Secondly, a broad definition is the best suited to the goals of my theoretical analyses: these are to assess the logical coherence of suggestions already present in the literature and to derive *qualitative* results regarding behavioural asymmetries and conflicts of interest between different parties. Thirdly, the definition of war as ‘coalitionary intergroup aggression’ applies to some non-human species as well (chimpanzees, spotted hyenas, wolves, and lions; Wrangham, 1999) and therefore allows discussion of how the results presented in this thesis might apply to beyond humans (e.g. Ch.3).

Evolutionary approaches to human behaviour

Three main evolutionary approaches to the study of human behaviour have developed since the 1970s and currently dominate the evolutionary behavioural sciences: evolutionary psychology, human behavioural ecology, and cultural evolution (including gene-culture coevolution; Laland and Brown, 2011; Mace, 2014; Glowacki, et al., 2017).

Evolutionary psychology investigates the cognitive mechanisms underlying human behaviour, hypothesising the existence of brain ‘modules’ (circuits or sets of circuits) that evolved to solve recurrent adaptive problems faced by our species during its long history of hunter-gatherer subsistence during the Pleistocene and Early Holocene (Barkow, et al., 1992; Laland and Brown, 2011; Glowacki, et al., 2017). As the ecological and social environment we live in today has changed drastically in the past fifteen millennia or so – especially since the development of agriculture and animal husbandry – the behaviours for which these modules are responsible might no longer be adaptive (thus generating ‘evolutionary mismatches’; Glowacki, et al., 2017).

Human behavioural ecology applies the methods of behavioural ecology (Davies, et al., 2012) to the study of human behaviour, focusing on functional and ultimate questions in Tinbergen’s schema (Tinbergen, 1963; Laland and Brown, 2011; Nettle, et al., 2013; Mace, 2014). It adopts an adaptive perspective, assuming that human behaviour evolves under the action of natural selection to maximise inclusive fitness (Hamilton, 1964; see following section) in given ecological conditions (Nettle, et al., 2013; Mace, 2014). It explores how the ecological context – broadly defined to include both the social and the physical environment – leads to the behavioural variation observed among human societies (Nettle, et al., 2013; Mace, 2014). The tools of human behavioural ecology are experimentation (when possible) or 'natural experiments', comparative studies, and mathematical modelling in the form of kin-selection or game-theoretic models (Mace, 2014; Glowacki, et al., 2017).

Proponents of cultural evolution (also known as gene-culture coevolution, or dual inheritance theory) argue that cultural change occurs in ways that are analogous – but not identical – to genetic evolution (Richerson and Boyd, 2005; Laland and Brown, 2011; Mesoudi, 2011, 2015; Creanza, et al., 2017; Glowacki, et al., 2017). This approach employs mathematical modelling based on the methodologies of population genetics theory (with early foundations laid by Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985)) to explore the effects of social transmission of cultural traits, which can be vertical (from parent to offspring), oblique (from non-parental adults) or horizontal (from peers) (Mesoudi, 2015; Creanza, et al., 2017). It also considers how genetic traits and cultural traits may interact and influence each other's evolution (e.g. coevolution of lactose tolerance and dairy farming; Mesoudi, 2015; Creanza, et al., 2017).

The nature of cultural evolutionary explanations – ultimate or proximate (Mayr, 1961; Tinbergen, 1963) – and their relation to behavioural ecological ones is controversial and has been much debated in recent years (Laland et al., 2011; Scott-Philips et al., 2011; Mace, 2014; Mesoudi, 2015). Numerous key figures in cultural evolution argue that cultural inheritance can be an ultimate cause of behaviour (Laland, et al., 2011; Mesoudi, 2015; Creanza, et al., 2017), and proponents of the Extended Evolutionary synthesis suggest that this argument applies to all forms of non-genetic inheritance (Laland et al., 2011, 2014). Other researchers, especially from the evolutionary psychology and human behavioural ecology traditions, argue instead that cultural evolutionary explanations are best seen as proximate, i.e. relating how a behaviour works, its 'mechanism' (Scott-Philips, et al., 2011; Mace, 2014). As both ultimate and proximate explanations are needed to obtain a full understanding of a behaviour (Tinbergen, 1963), Mace (2014) argues that both behavioural ecological approaches and cultural evolutionary approaches are valuable – and indeed hard to distinguish – when testing hypotheses in the real world.

In this thesis, I take a behavioural ecological approach to warfare – the human behaviour I investigate here – developing mathematical models with the tools of social evolution theory, especially the kin selection framework, whose results admit an inclusive fitness interpretation (Hamilton, 1964; Frank, 1998; Bourke, 2011; see section directly below). However, in the discussion sections of Chapters 2-5 and in the general thesis Discussion provided in Chapter 6, I consider the effects of cultural change and its potential interaction with genetic change – in the conviction that genes and culture are not alternative explanations for human behaviour, but are closely intertwined (cf. Mace, 2014).

Social evolution theory: themes, methods and open questions

Social evolution theory investigates the evolution of social behaviours (West, et al, 2007a). Such behaviours are performed during interactions between two or more individuals, and have an impact not only on the reproductive success of the individual performing them (the ‘actor’), but also on that of other individuals with which they interact (the ‘recipients’). They can thus be classified on the basis of their effects on the fitness of the actor and the recipient (Hamilton, 1964; West et al., 2007a; see Fig. 1.1). A social behaviour is ‘mutually beneficial’ if both the fitness of the actor and that of the recipient are increased as a result of it, while it is ‘selfish’ if it increases the fitness of the actor and decreases that of the recipient. On the other hand, a behaviour that decreases the fitness of the actor is either ‘altruistic’ or ‘spiteful’, depending on whether it increases or decreases the fitness of the recipient, respectively. It is important to notice that, in the context of the study of human social behaviour, there has been considerable controversy around the use of some of these

		Effect on recipient	
		+	–
Effect on actor	+	Mutual benefit	Selfishness
	–	Altruism	Spite

Figure 1.1 – Classification of social behaviours based on the effect on the fitness of the actor and of the recipient (Hamilton, 1964; West et al., 2007a)

terms (reviewed in West, et al., 2011). For example, in recent years, the term 'altruism' has been redefined by some authors to describe behaviours that provide direct benefits to the actor and are thus, in reality, mutually beneficial (e.g. Gintis, 2000). This has caused considerable confusion (West, et al., 2011). To avoid such confusion and to allow comparison with previous work, here I adopt the definitions presented above, as they are simple and general, they are the most widely accepted in social evolution theory (West, et al., 2007a, 2011) and have been introduced early in the development of the theory (Hamilton, 1964).

Behaviours that involve a direct fitness benefit for the actor are easily explained. Altruism, however, was not explained satisfactorily in evolutionary terms until the development of inclusive fitness theory (Hamilton, 1964); this same framework was later employed to explain spiteful behaviours (Hamilton, 1970). Since the foundational work of W. D. Hamilton, different approaches to modelling social evolution problems have developed (reviewed in Wenseleers et al., 2010), resulting in a great flourishing of the discipline, also thanks to a fruitful synergy with empirical research (West et al., 2007b). Two main theoretical frameworks exist: kin selection and multilevel selection (Wenseleers et al., 2010; West and Gardner, 2013).

Kin selection

The fundamental insight of kin selection theory is that any behaviour, be it social or non-social, will be favoured by selection when the following mathematical statement, known as 'Hamilton's rule', is satisfied: $-c + b\,R > 0$, where c is the fitness cost to the actor, b is the fitness benefit to the recipient, and R is the genetic relatedness between the two individuals

(Hamilton, 1963, 1964, 1970; Charnov, 1977; see also Gardner, 2015a). Two different approaches within kin selection theory, both introduced by Hamilton (1964, 1970, 1975) lead to this result: the neighbour-modulated fitness approach and the inclusive fitness approach.

The neighbour-modulated fitness approach is ‘recipient-based’, in that it focuses on the personal fitness of an individual as influenced by its own genotype (direct fitness effect) and the genotypes of their neighbours (indirect fitness effect) (Fig. 1.2a). In this context, the *c* term of Hamilton’s rule represents the fitness cost paid by the focal individual for performing the behaviour, the *R* term is conceptualised as the correlated tendency of social partners to help the focal individual, and the *b* term is the benefit the focal individual receives if helped (Hamilton, 1964; Frank, 1998).

On the other hand, the inclusive fitness approach is ‘actor-based’, focusing on how a focal individual impacts on their own fitness (direct fitness) and on the fitness of their social partners (indirect fitness) (Fig. 1.2b). An altruistic behaviour leads to an increase in the actor’s inclusive fitness if the decrease in personal reproduction due to the behaviour is more than outweighed by an increase in the reproduction of social partners, the latter being weighted by genetic relatedness of the actor to these social partners. In this case, the *c* term of Hamilton’s rule still represents the fitness cost paid by the focal individual, but the conceptualisation of *b* and *R* is different. The *b* term represents the fitness benefit the actor provides to their social partners, while *R* measures how valuable the fitnesses of social partners are to the actor (Hamilton, 1964; Frank, 1998).

As mentioned above, the two methods are entirely equivalent and both can be readily expanded to allow the study of class-structured populations (e.g. sex or age classes;

Wenseleers, et al., 2010). The neighbour-modulated fitness approach is the one most often used to model specific questions and develop new theory, because it offers the most direct way to obtain predictions (West and Gardner, 2013). This approach has been rendered particularly powerful and successful by the introduction of the 'Taylor-Frank method' for evaluating impacts of selection, which assumes vanishingly small genetic variation and weak selection (Taylor and Frank, 1996) (Box 1.3). On the other hand, the inclusive fitness approach is used for conceptualisation and in empirical studies, because inclusive fitness is the quantity that organisms appear designed to maximise (West and Gardner, 2013).

Box 1.3 – The Taylor-Frank method

The Price equation (Price 1970) states that the change in the genic value $\Delta_{\mathrm{NS}}\bar{g}$ of a given gene between generations due to natural selection is equal to the covariance between the relative fitness of the individual W and the genic value g. In turn, provided there is non-zero genetic variance, this is equal to the product of the regression of fitness on genic value and the genetic variation. In mathematical form:

$$\Delta_{\mathrm{NS}}\bar{g} = \mathrm{cov}(W, g) = \beta(W, g)\ \mathrm{Var}(g)$$

Under the assumption of weak selection and vanishingly small genetic variation, we can approximate $\beta(W, g)$ to $\mathrm{d}W/\mathrm{d}g$ (Taylor and Frank, 1996; Taylor, 1996). The condition for an increase in the trait associated with the gene under study is given by $\mathrm{d}W/\mathrm{d}g > 0$ (Taylor and Frank, 1996; Taylor, 1996).

Following the neighbour modulated fitness approach, the Taylor-Frank method describes the fitness of the focal individual as a function of their own phenotype x and the average phenotype of their social partners y (Taylor and Frank, 1996; Taylor, 1996). Applying differential calculus methods, the condition for increase becomes:

$$\frac{\partial W}{\partial x}\frac{\mathrm{d}x}{\mathrm{d}G}\frac{\mathrm{d}G}{\mathrm{d}g}+\frac{\partial W}{\partial y}\frac{\mathrm{d}y}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g}>0$$

where G is the breeding value of the focal individual, G' is average breeding value of their social partner, $\partial W/\partial x$ is the impact of an individual's own phenotype on their own fitness and can be conceptualised as a fitness cost ($-c$), $\partial W/\partial y$ is the impact of the average social partner on the focal individual and can be conceptualised as a fitness benefit (b), $\mathrm{d}x/\mathrm{d}G$ and $\mathrm{d}y/\mathrm{d}G'$ describe the correlation between an individual's breeding value and their own phenotype and are assumed to be equal, $\mathrm{d}G/\mathrm{d}g = p$ is the consanguinity of an individual to themselves, and $\mathrm{d}G'/\mathrm{d}g = p'$ is the consanguinity of the focal individual to a random social partner (Bulmer, 1994). Considering that the genetic relatedness between a focal individual and her social partner is $R = p/p'$, we recover Hamilton's rule: $-c + b R > 0$ (Hamilton, 1963; 1964; 1970). This method can be readily extended to consider more than one recipient (Grafen, 2006; Gardner, 2012).

The Taylor-Frank method can be readily applied to class-structured populations. In this case, selection within each class is analysed separately and the total action of natural selection is given by the sum of all the derivatives of fitness over genic value, weighing each component by that class's reproductive value (Fisher, 1930; Price, 1970; Price and Smith, 1972). For example, the condition for an increase in the genic value g in a sex-structured population is given by:

$$c_{\mathrm{f}}\frac{\mathrm{d}W_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}}+c_{\mathrm{m}}\frac{\mathrm{d}W_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{m}}}>0$$

where subscripts f and m indicate males and females, respectively, and c_{m} and c_{f} are the class reproductive values for males and females, respectively. Under diploidy, male and females have identical class reproductive values, $c_{\mathrm{m}} = c_{\mathrm{f}} = 1/2$ (Fisher, 1930; Price, 1970; Price and Smith, 1972; Taylor, 1996).

Multilevel selection

In contrast to kin selection, multilevel selection theory (also known as 'group selection' or 'levels-of-selection' theory) tackles the question of social behaviours in terms of selection within and between groups (Price, 1972; Hamilton, 1975; Okasha, 2006) (Fig. 1.2c). Within-group selection favours the spread of selfish behaviours, while between-group selection favours altruism, because groups with more cooperators will prevail in group-group competition: therefore, the final outcome depends on the relative strength of the two forces at play (Hamilton, 1975).

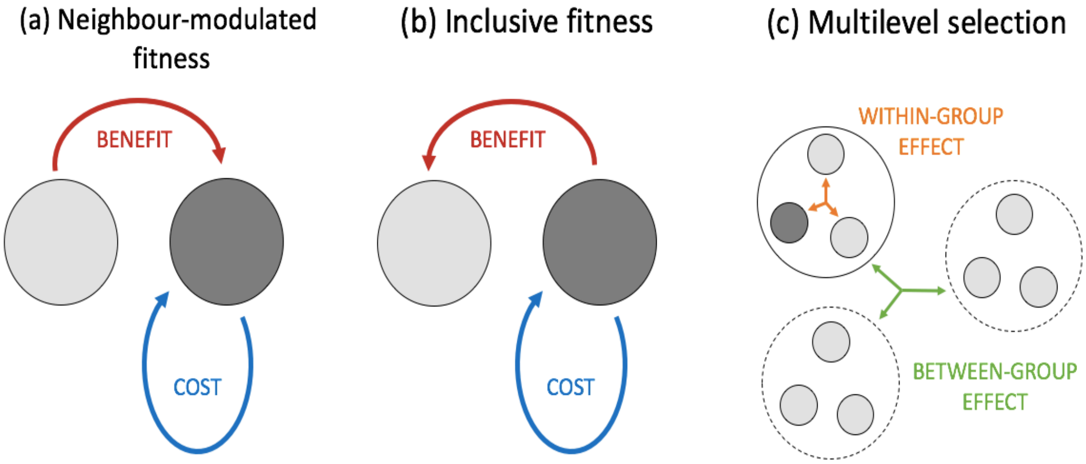

Figure 1.2 – Three equivalent approaches to the study of social evolution. (a) Neighbour-modulated fitness approach. The fitness of the focal individual (darker circle) is decreased (-*c*, blue arrow) as a result of her own genotype and is increased (*b*, red arrow) as a result of the genotype of her social partner (lighter circle). (b) Inclusive fitness approach. A focal individual with an altruistic genotype (darker circle) incurs in a direct fitness cost (-*c*, blue arrow), but provides a fitness benefit (*b*, red arrow) to her social partner (lighter circle), to whom she might be genetically related. (c) Multilevel selection. The fitness of the focal individual (darker circle) is influenced both by within-group effects (orange arrows) and between-group effects (green arrows). Diagram based on Wenseleers et al. (2010) and West and Gardner (2013).

In the past, this approach was seen as describing a different biological process from kin selection and was perceived as a competing hypothesis for the explanation of altruism (e.g Wilson, 1975). This led to the 'levels-of-selection' debate (reviewed in Okasha, 2006), which was concerned with understanding at what level of the biological hierarchy natural selection acts. Most workers agree that the controversy is now over, because kin selection and group selection have been demonstrated to be equivalent (Hamilton, 1975; Frank, 1985, 1986; see also West and Gardner, 2013). Both approaches are derived from Price's theorem (Price, 1970, 1972), a simple mathematical statement that describes the change of any evolving entity under the action of selection. However, the group selection approach is not often used by theoreticians, because its methodology is cumbersome and does not readily support class-structure (Gardner, 2015b), meaning that populations with different kinds of individuals (e.g. differing by sex, age, or habitat) are difficult to analyse. For example, all major advances in local mate competition theory, an important area of social evolution, have employed the kin selection approach (West, et al., 2008).

Units of adaptation controversy

Still very controversial is the level of the biological hierarchy at which adaptations occur. This is a separate question from that of the levels of selection (Gardner and Grafen, 2009) and it is of great significance, because it is linked to explaining 'major evolutionary transitions' (Maynard Smith and Szathmáry, 1995; Bourke, 2011). During major transitions in individuality, previously-independent units merge and become interdependent, forming new individualities, which constitute new units of adaptation (Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1995). The study of such shifts – which include the transition from molecular replicators to cellular life, from individual cells to multicellular organisms, and from simple to complex human societies – has generated a very rich body of work in the past two decades (Szathmáry, 2015; West, et al., 2015).

Conventionally, adaptations are seen as functioning for the good of the individual (Darwin, 1859). Inclusive fitness theory reinforced this view and made it dominant by clarifying the true nature of Darwinian fitness: adaptations maximise the inclusive fitness of the individual (Hamilton, 1964, 1970). A first alternative to this is the 'selfish gene' view of Dawkins (1976), who maintains that adaptation is best viewed at the level of the gene. Gardner and Welch (2011) provided formal justification for this idea, underlining that the gene is in fact maximising its inclusive, not personal, fitness. This means that the gene will strive to maximise the number of copies of itself in the following generation both through personal reproduction and through the reproduction of identical genes in other individuals (Gardner and Welch, 2011). The second alternative, which has undoubtedly generated more debate than the former, is the idea that social behaviours evolve for the good of the group and are therefore 'group-level adaptations' (e.g. Wynne-Edwards, 1962). Gardner and Grafen (2009) developed formal theory on the subject and showed that such adaptations are possible, but only under very restrictive conditions, namely that within-group competition be completely absent (see also Gardner, 2015b).

Genomic imprinting

In recent years, a resurgence in interest in genomic imprinting and the study of its drivers and consequences has stimulated new questions in the units of adaptation debate (e.g. Gardner, 2014). Genomic imprinting is an epigenetic phenomenon consisting in parent-of-origin-specific expression of genes, such that the heterozygous genotypes Aa and aA – where the first position represents the maternal-origin gene, while the second is paternal-origin – do not lead to identical phenotypes as in classical Mendelian genetics (Reik and Walter, 2001). Typically, one gene is silenced, while the other is expressed, rendering the locus functionally haploid and exposing the individual to the deleterious effects of mutations (see Falls et al., 1999; Hirasawa and Feil, 2010, for reviews of imprinting disorders in humans).

The most developed and widely-accepted explanatory framework for genomic imprinting is the ‘conflict theory’, also known as ‘kinship theory’ (Haig, 2002; Brandvain, et al., 2011). This is based on inclusive fitness theory and proposes that genomic imprinting is the result of a conflict between paternal-origin and maternal-origin genes, when these are differentially related to the individuals with whom their carrier interacts (Haig, 1996, 1997). For example, if interactions occur between maternal siblings who are not also paternal siblings, maternal-origin genes are more related to the social partners of their carrier than are the paternal-origin genes. In the case of a locus underlying an altruistic behaviour, maternal-origin genes will favour a higher level of altruism, while paternal-origin genes will favour a lower one. The conflict theory predicts that, as a consequence of this conflict of interest, maternal-origin genes will upregulate their expression, while paternal-origin genes will downregulate their expression (Haig, 1996, 1997). The result of this evolutionary escalation is genomic imprinting: in our example situation, paternal-origin genes will ultimately silence themselves, thus losing the conflict, while maternal-origin genes will reach their optimal level of expression, thus winning the conflict (‘loudest-voice-prevails principle’; Haig, 1996). The explanation provided by the conflict theory shows how genomic imprinting constitutes a particularly fruitful area of enquiry for social evolution theory: in this context, considering a locus underlying a social behaviour, the interests of genes, individuals and groups are pitted against each other (Gardner, 2014).

Alternative explanations for genomic imprinting, which do not invoke conflicts of interest between different parties, have been suggested over the years. These were recently reviewed by Spencer and Clark (2014) who identified thirteen of them (see also Wilkins and Haig, 2003). Most of these are not supported by empirical evidence and/or theoretical work shows that they are not feasible explanations or they could apply only to very limited scenarios (Spencer and Clark, 2014). It is, however, worth discussing two of these hypotheses which, in my estimation, have received the most attention in recent years and might hold some explanatory potential.

The 'maternal-foetal coadaptation' theory suggests that genomic imprinting allows the gene products of a juvenile and its mother to match (or differ) systematically, greatly increasing the fitness of the former (Wolf and Hager, 2006; 2009; reviewed in Spencer and Clark, 2014). Recent experimental work on imprinted loci in mice by Cowley, et al. (2014) was interpreted by the authors as evidence for 'maternal-foetal coadaptation' (see also Wolf et al., 2015). This view was questioned by Úbeda and Gardner (2015), who showed that the expression patterns identified in the study were actually in line with kinship theory predictions, not with those of the coadaptation theory. Nonetheless, the 'maternal-foetal coadaptation' deserves additional theoretical exploration to clarify its predictions and would benefit from additional testing against experimental data.

The second hypothesis that could possibly hold some explanatory potential is the 'co-adaptation of gene expression' theory, proposed by Wolf (2013) (reviewed in Spencer and Clark, 2014). This suggests that loci that interact with an imprinted locus should be favoured by selection to evolve imprinting in that same direction, because this allows expression of alleles inherited from the same parent (Wolf, 2013). This hypothesis offers an explanation for why imprinted genes often appear in clusters, but may not apply in general, as many clusters have genes imprinted in different directions (Spencer and Clark, 2014). In addition, it does not illuminate the origin of the first imprinted locus (Spencer and Clark, 2014), which is instead more satisfactorily explained by the kinship theory.

2 Intrafamily and intragenomic conflicts in human warfare[‡]

It’s always the old that lead us to the war
It’s always the young to fall

–Phil Ochs, *I Ain’t Marching Anymore*

Abstract

Recent years have seen an explosion of multidisciplinary interest in ancient human warfare. Theory has emphasised a key role for kin-selected cooperation, modulated by sex-specific demography, in explaining intergroup violence. However, conflicts of interest remain a relatively underexplored factor in the evolutionary-ecological study of warfare, with little consideration given to which parties influence the decision to go to war and how their

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motivation may differ. We develop a mathematical model to investigate the interplay between sex-specific demography and human warfare, showing that: the ecology of warfare drives the evolution of sex-biased dispersal; sex-biased dispersal modulates intrafamily and intragenomic conflicts in relation to warfare; intragenomic conflict drives parent-of-origin-specific patterns of gene expression – i.e. “genomic imprinting” – in relation to warfare phenotypes; and an ecological perspective of conflicts at the levels of the gene, individual and social group yields novel predictions as to pathologies associated with mutations and epimutations at loci underpinning human violence.

Introduction

Recent years have seen an explosion of interest in ancient human warfare (Kelly, 2005; Fry, 2006; 2007; Gat, 2006; Choi and Bowles, 2007; Smirnov et al., 2007; Lehmann and Feldman, 2008; Bowles, 2009; Wrangham and Glowacki, 2012; Ferguson, 2013; Fry and Söderberg, 2013; Turchin et al., 2013; Johnson and Toft, 2014; Glowacki and Wrangham, 2015; Low, 2015; Turchin, 2015; Zefferman and Mathew, 2015; Lopez, 2016). Discoveries of prehistoric mass graves and other striking evidence of lethal intergroup conflict have challenged a traditional view that our ancestors were relatively peaceful (Teschler-Nicola, 2012; Wahl and Trautmann, 2012; Meyer et al., 2015; Mirazón Lahr et al., 2016) and has spurred strong multidisciplinary effort into understanding the incentives for human intergroup violence (Ferguson, 2000; Gat, 2000a; 2000b; Gat, 2006; Wrangham and Glowacki, 2012; Johnson and Toft, 2014; Lopez, 2016). Although quantitative theoretical progress on this topic has been relatively slow, analysis of mathematical models has yielded a number of important insights into the evolutionary and ecological drivers of war. In particular, Lehmann & Feldman's (2008) study of the evolution of belligerence and bravery behaviours, in the context of a population model with sex-specific demography, has highlighted a possible key role for kin selection in incentivising adolescent males to altruistically cooperate in warfare – paying personal costs, but yielding benefits, such as additional resources or mating opportunities, for their groupmates – even in the context of large groups (where average within-group relatedness is low).

Paradoxically, conflicts of interest remain a relatively neglected factor in the evolutionary-ecological study of human intergroup violence, with little consideration given to which parties influence the decision to go to war and how these various parties' interests might differ. For instance, whilst Lehmann & Feldman (2008) assumed that each adolescent male's behaviour is determined by his father's genotype, such that it is the inclusive fitness interests of the father that govern the son's belligerence and bravery in relation to warfare, the son's own interests are liable to be different from his father's, especially in relation to selfless acts that may benefit his siblings but incur a severe personal cost. This suggests the potential for parent-offspring conflict (*sensu* Trivers, 1974). Moreover, the interests of the individual's mother are also liable to differ from those of the father, owing to sex-specific demographic factors – such as sex-biased dispersal – that are expected to generate sex differences in relatedness to groupmates, suggesting the possibility for sexual conflict (*sensu* Trivers, 1972). Furthermore, sex-specific demographic processes have been shown to drive conflicts of interest between an individual's maternal-origin and paternal-origin genes with respect to social behaviour (Haig, 2000; Úbeda and Gardner, 2010; 2011; 2012; Úbeda et al., 2014; Farrell et al., 2015), and accordingly there may even be intragenomic conflict (*sensu* Burt and Trivers, 2006), of a form that has been implicated in the evolution of parent-of-origin-specific gene expression, or "genomic imprinting" (Haig 1996, 2002; Reik and Walter, 2001). This renders individuals vulnerable to a range of debilitating cognitive, behavioural and growth disorders (Falls, et al., 1999), some of which have been linked with aggression and violence (Strachan, et al., 2009; Thibert, et al, 2013; Powis and Oliver, 2015). However, such conflicts of interest remain underexplored.

Here, we determine the scope for – and consequences of – parent-offspring conflict, sexual conflict and intragenomic conflict in relation to warfare. We reformulate and generalise Lehmann & Feldman's (2008) model to consider control of belligerence and bravery by either the adolescent male, his mother, his father, his maternal-origin genes or his paternal-origin genes. We use this extended model to investigate: (a) the evolution of sex-specific dispersal in the context of the ecology of warfare; (b) how sex-biased dispersal modulates intrafamily and intragenomic conflicts in relation to warfare; (c) how intragenomic conflicts of interest can drive genomic imprinting (Reik and Walter, 2001); and (d) the phenotypic and pathological consequences of different classes of mutation and epimutation at imprinted loci underpinning intergroup violence phenotypes.

Methods

Following Lehmann & Feldman (2008), we consider a large population separated into groups of N_f adult females and N_m adult males, connected by random migration. At the beginning of the life cycle, each adult female produces a large number K_f of daughters and a large number K_m of sons, then dies, and her offspring mature to become subadults. Each subadult disperses away from their natal group with probability d_f for females and d_m for males, and each disperser dies in the process with probability λ_f for females and λ_m for males, with survivors arriving at random groups. Accordingly, following dispersal, the probability that an individual is a migrant is $m_f = d_f(1 - \lambda_f)/(1 - d_f\lambda_f)$ for females and $m_m = d_m(1 - \lambda_m)/(1 - d_m\lambda_m)$ for males. In every generation, each post-dispersal group is in a position to attack one randomly chosen group – which it does with probability $a(A_{att})$, where A_{att} is the average level of belligerence exhibited by subadult males in the attacking group and $\partial a/\partial A_{att} = b_a$ is the marginal increase in the probability of the group attacking another – and to be attacked by one other group. If war is initiated, the attacking group wins with probability $\omega(\Omega_{att}, \Omega_{def})$, where Ω_{att} and Ω_{def} are the average levels of bravery exhibited by subadult males in the attacking and defending groups, respectively, and where $\partial\omega(\Omega_{att}, \Omega_{def})/\partial\Omega_{att} = b_\omega$ is the marginal increase in the probability of the attackers winning the war (for simplicity, we assume that bravery is equally important in defence: $\partial\omega(\Omega_{att}, \Omega_{def})/\partial\Omega_{def} = -b_\omega$). Following warfare: in non-attacked groups, individuals compete for breeding positions against their same-sex groupmates, each subadult male having competitiveness $t(A_{ind})$, where A_{ind} is his level of belligerence and $-(\partial t(A_{ind})/\partial A_{ind})/t(\bar{A}) = c_a$ is the competitive cost of belligerence; in groups that successfully defend themselves from attack, individuals compete for breeding positions against their same-sex groupmates, each subadult male having competitiveness $t(A_{ind}) \cdot \tau(\Omega_{ind})$, where Ω_{ind} is his level of bravery and $-(\partial\tau(\Omega_{ind})/\partial\Omega_{ind})/\tau(\bar{\Omega}) = c_\omega$ is the competitive cost of bravery; and in conquered groups, individuals compete for breeding positions against their same-sex groupmates and their same-sex attackers, each subadult male having competitiveness $t(A_{ind}) \cdot \tau(\Omega_{ind}) \cdot s_m$ if they belong to the defeated group and $t(A_{ind}) \cdot \tau(\Omega_{ind}) \cdot (1 - s_m)$ if they belong to the conquering group, and each subadult female having a competitiveness s_f if they belong to the defeated group and $1 - s_\mathrm{f}$ if they belong to the conquering group. That is, whilst a male's belligerence phenotype is always expressed and always incurs a competitive cost, his bravery phenotype is only expressed and only incurs a competitive cost when his group attacks or is attacked by another group. We perform a kin-selection analysis (Hamilton, 1964; Taylor, 1996; Taylor and Frank, 1996; Frank, 1997; 1998; Rousset, 2004; Taylor et al., 2007) to determine how selection acts upon female dispersal, male dispersal, belligerence and bravery (see Extended Methods for details).

Results

Sex-biased dispersal

Sex-biased dispersal is observed in many taxa and, on the basis of population genetic data (Seielstad, et al., 1998) and dispersal patterns of African apes (Lawson Handley and Perrin, 2007) and modern hunter-gatherers (Ember, 1978), it is understood that female-biased dispersal (patrilocality) was the ancestral condition for humans (Úbeda and Gardner, 2011). However, the causes of these patterns remain unclear and are much debated: theoretical work has identified possible drivers of sex-biased dispersal in mating systems, inbreeding avoidance and competition and cooperation between kin (reviewed in Lawson Handley and Perrin, 2007; see also Clutton-Brock and Lukas, 2012) and many anthropologists have focused on the greater importance of kin recognition and associated cooperation between male kin to explain patrilocality (reviewed in Marlowe, 2004). Here, we investigate the evolution of sex-specific dispersal in a population undergoing recurrent acts of war.

Predictably, we find that sex differences in the mortality cost of dispersal can drive sex-biased dispersal (Fig. 2.1a). More surprisingly, we find that the ecology of warfare itself (Low, 2015) can drive the evolution of sex-biased dispersal even when the mortality cost of dispersal is the same for individuals of each sex (Fig. 2.1b).

Inclusive fitness is the sum of an individual's direct fitness (accrued through their impact on their own fitness) and indirect fitness (accrued through their impact on the fitness of their genetic relatives; Hamilton, 1964). A subadult female increases her inclusive fitness by dispersing away from her natal group when:

$$-\lambda_{\mathrm{f}} + \big(1 - 2\bar{a}\bar{\omega}s_{\mathrm{f}}(1 - s_{\mathrm{f}})\big)(1 - m_{\mathrm{f}})\, r_{\mathrm{female}} > 0, \qquad [2.1]$$

where $\bar{a} = a(\bar{A})$ is the population average probability of a group initiating war, $\bar{\omega} = \omega(\overline{\Omega}, \overline{\Omega})$ is the population average probability of the group winning the war, and r_{female} is the subadult female's relatedness to other females born in her natal group. That is, she suffers a direct-fitness cost (first term in condition [2.1]), owing to the probability λ_{f} of dying on the way to to her new group. And she receives an indirect-fitness benefit (second term), owing to the relaxation of competition for breeding positions among females, to whom she may be genetically related, in her natal group. Specifically: with probability $1 - 2\bar{a}\bar{\omega}s_{\mathrm{f}}(1 - s_{\mathrm{f}})$ the female who wins the breeding position that she might otherwise have taken derives from her natal group, post-dispersal, as opposed to an attacking group; with probability $1 - m_{\mathrm{f}}$ a female in her natal group, post-dispersal, was born in that same group, as opposed to migrating from elsewhere; and the relatedness between two females born in the same group is r_{female}. Note that the fitness effects in condition [2.1] are correct up to a scaling factor that cancels out of the expression. An intermediate, convergence-stable (Taylor, 1996; Davies and Gardner, 2016) level of female dispersal d_{f}^{*} obtains when the left-hand side left-hand side of condition [2.1] equals zero.

Analogously, a subadult male increases his inclusive fitness by dispersing away from his natal group when:

$$-\lambda_{\mathrm{m}} + \left(1 - 2\bar{a}\bar{\omega}s_{\mathrm{m}}(1 - s_{\mathrm{m}})\right)(1 - m_{\mathrm{m}})\, r_{\mathrm{male}} > 0, \tag*{[2.2]}$$

where r_{male} is his relatedness to the other males born in his natal group. An intermediate, convergence-stable level of male dispersal d_{m}^{*} obtains when the left-hand side of condition [2.2] equals zero.

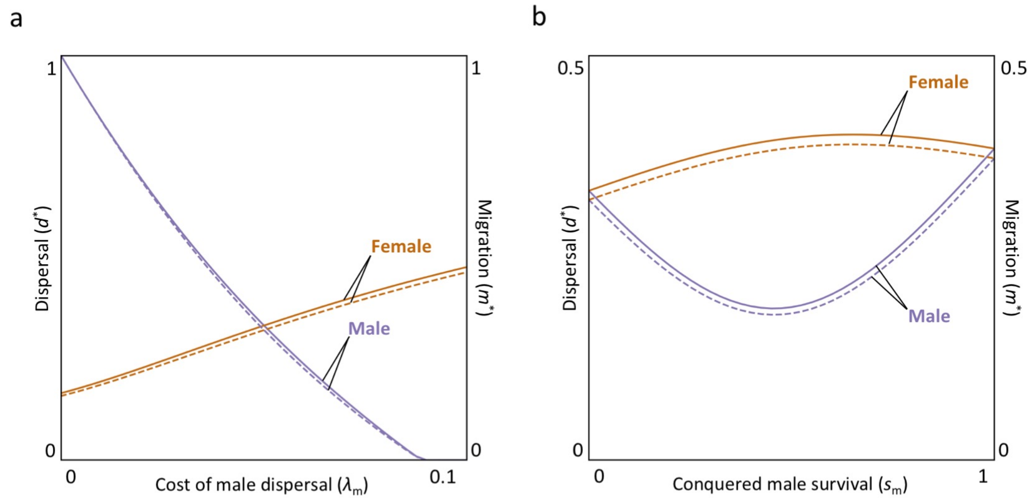

Figure 2.1 - Evolution of sex-biased dispersal and migration. Convergence-stable levels of female dispersal (d_{f}^{*}, solid orange line), male dispersal (d_{m}^{*}, solid purple line), female migration (m_{f}^{*}, dashed orange line) and male migration (m_{m}^{*}, dashed purple line) as a function of cost of male dispersal (λ_{m}; panel a; other parameter values are $\lambda_{\mathrm{f}} = 0.05$, $s_{\mathrm{f}} = 1$, $s_{\mathrm{m}} = 0$, $N_{\mathrm{f}} = N_{\mathrm{m}} = 10$, $\bar{a} = 1$, $\bar{\omega} = 0.5$) and the probability that a conquered male obtains a breeding spot (s_{m}; panel b; other parameter values are $\lambda_{\mathrm{f}} = \lambda_{\mathrm{m}} = 0.05$, $s_{\mathrm{f}} = 1$, $N_{\mathrm{f}} = N_{\mathrm{m}} = 10$, $\bar{a} = 1$, $\bar{\omega} = 0.5$).

Inspection of conditions [2.1] and [2.2] reveals that sex-biased dispersal may be favoured in two different ways. Firstly, the direct-fitness cost of dispersal may differ for the two sexes ($\lambda_{\mathrm{f}} \neq \lambda_{\mathrm{m}}$) such that, all else being equal, dispersal is more favoured in the sex with the lower cost (i.e. $d_{\mathrm{f}}^{*} \geq d_{\mathrm{m}}^{*}$ if $\lambda_{\mathrm{f}} \leq \lambda_{\mathrm{m}}$ and $d_{\mathrm{f}}^{*} \leq d_{\mathrm{m}}^{*}$ if $\lambda_{\mathrm{f}} \geq \lambda_{\mathrm{m}}$; Fig. 2.1a). This sex bias in dispersal translates into a sex bias in migration, in the same direction (Fig. 2.1a). Secondly, even if the direct-fitness cost is the same for both sexes (i.e. $\lambda_{\mathrm{f}} = \lambda_{\mathrm{m}}$), the indirect-fitness benefit of dispersal may differ for the two sexes, owing to sex differences in the ecology of warfare. Specifically, denoting the extent to which the mothers of offspring born in a conquered group are a mixture of individuals from that group and from the conquering group ('maternal admixture') by $M_{\mathrm{f}} = s_{\mathrm{f}}(1 - s_{\mathrm{f}})$, and the extent to which the fathers of offspring born in a conquered group are a mixture of individuals from that group and from the conquering group ('paternal admixture') by $M_{\mathrm{m}} = s_{\mathrm{m}}(1 - s_{\mathrm{m}})$, then – all else being equal – dispersal is more favoured in the sex with the lowest degree of admixture (i.e. $d_{\mathrm{f}}^{*} \geq d_{\mathrm{m}}^{*}$ if $M_{\mathrm{f}} < M_{\mathrm{m}}$ and $d_{\mathrm{f}}^{*} \leq d_{\mathrm{m}}^{*}$ if $M_{\mathrm{f}} > M_{\mathrm{m}}$; Fig. 1b). This sex bias in dispersal translates into a sex bias in migration, in the same direction (Fig. 2.1b). For example, if half of all offspring born into conquered groups are fathered by males of the conquered group and the other half are fathered by males from the conquering group (i.e. $s_{\mathrm{m}} = 0.5$), but the mothers of all of these offspring are from the conquered group (i.e. $s_{\mathrm{f}} = 1.0$), then there is less maternal admixture (i.e. $M_{\mathrm{f}} = 0.0$) than there is paternal admixture (i.e. $M_{\mathrm{m}} = 0.25$) and, consequently, females are relatively more favoured to disperse than are males (i.e. $d_{\mathrm{f}}^{*} > d_{\mathrm{m}}^{*}$). In this instance, a dispersing female is relatively more likely (and a dispersing male relatively less likely) to free up a breeding position for a relative, such that females obtain greater indirect-fitness benefits from dispersing. We confirm the robustness of these analytical results using individual-based simulations (see Extended Methods for details).

Belligerence and bravery

The propensity of a group to go to war is determined by the average belligerence of its subadult males; and success in war is linked to these males' average bravery. However, although these two traits are expressed in subadult males, they may be controlled by various parties – including the male himself, his mother, his father, his maternal-origin genes and his paternal-origin genes – whose inclusive-fitness interests may disagree with each other (intrafamily and intragenomic conflict). To assess the interests of these various parties, we hypothetically grant full control to each of them, in turn, and assess when an increase in the male's trait leads to an increase in the controller's inclusive fitness. We first describe the inclusive-fitness consequences of these traits under the influence of a general controller, before focusing on each control option in turn.

Participation in warfare implies fitness costs for the subadult male, but may result in fitness benefits for his subadult groupmates. Accordingly, the controller of the male's behaviour may derive an overall inclusive-fitness benefit by increasing his participation in warfare, depending upon how closely related the controller is to the male and how closely related the controller is to the male's groupmates. Specifically, the controller increases their inclusive fitness by increasing the male's level of belligerence when:

$$-c_{\mathrm{a}} + \left(1 - 2\,\bar{a}\,\bar{\omega}\,s_{\mathrm{m}}\,(1 - s_{\mathrm{m}})\right) c_{\mathrm{a}}\,R_{\mathrm{male|controller}} + \bar{\omega}\,\left((1 - s_{\mathrm{m}})\,R_{\mathrm{male|controller}} + (1 - s_{\mathrm{f}})\,R_{\mathrm{female|controller}}\right) b_{\mathrm{a}} > 0, \qquad [2.3]$$

where $R_{\mathrm{male|controller}}$ is the relatedness of the controller to a random male groupmate of the focal male, expressed relative to the controller's relatedness to the focal male himself, and $R_{\mathrm{female|controller}}$ is the relatedness of the controller to a random female groupmate, expressed relative to the controller's relatedness to the focal male himself. That is, an increase in the focal male's belligerence leads: to an inclusive-fitness cost (first term in condition [2.3]), owing to the focal male's loss of competitiveness $-c_{\mathrm{a}}$ for breeding positions; an inclusive-fitness benefit (second term), owing to the c_{a} vacated breeding positions being occupied by other males, who are derived from the same group with probability $1-2\,\bar{a}\,\bar{\omega}\,s_{\mathrm{m}}\,(1-s_{\mathrm{m}})$ and, in which case, are related to the controller by $R_{\mathrm{male|controller}}$; an inclusive-fitness benefit (third term), owing to the increased probability b_{a} of going to war, which is won with probability $\bar{\omega}$ and consequently yields an extra $1-s_{\mathrm{m}}$ breeding success for male groupmates who are related to the controller by $R_{\mathrm{male|controller}}$ and an extra $1-s_{\mathrm{f}}$ breeding success for female groupmates who are related to the controller by $R_{\mathrm{female|controller}}$. Again, the fitness effects in condition [2.3] are correct up to a scaling factor that cancels out. Providing it takes an intermediate value, the convergence-stable level of belligerence is obtained by setting the left-hand side of condition [2.3] equal to zero and solving for $\bar{A} = A^*_{\mathrm{controller}}$, which may be interpreted as the controller's belligerence optimum.

Similarly, the controller increases their inclusive fitness by increasing the male's level of bravery when:

$$-c_{\omega} + \left(1 - 2\bar{\omega}s_{\mathrm{m}}(1-s_{\mathrm{m}})\right)c_{\omega}R_{\mathrm{male|controller}} + 2\left((1-s_{\mathrm{m}})R_{\mathrm{male|controller}} + (1-s_{\mathrm{f}})R_{\mathrm{female|controller}}\right)b_{\omega} > 0. \qquad [2.4]$$

That is, an increase in the focal male's bravery leads: to an inclusive-fitness cost (first term in condition [2.4]), owing to the focal male's loss of competitiveness $-c_{\omega}$ for breeding positions; an inclusive-fitness benefit (second term), owing to the c_{ω} vacated breeding positions being occupied by other males, who are derived from the same group with probability $1 - 2\,\bar{\omega}\,s_{\mathrm{m}}\,(1 - s_{\mathrm{m}})$ and, in which case, are related to the controller by $R_{\mathrm{male|controller}}$; an inclusive-fitness benefit (third term), owing to the increased probability b_{ω} of winning a war and consequently yielding an extra $1 - s_{\mathrm{m}}$ breeding success for male groupmates who are related to the controller by $R_{\mathrm{male|controller}}$, and an extra $1 - s_{\mathrm{f}}$ breeding success for female groupmates who are related to the controller by $R_{\mathrm{female|controller}}$. Once again, the fitness effects in condition [2.4] are correct up to a scaling factor. Providing it takes an intermediate value, the convergence-stable level of bravery is obtained by setting the left-hand side of condition [2.4] equal to zero and solving for $\bar{\Omega} = \Omega^{*}_{\mathrm{controller}}$, which may be interpreted as the controller's bravery optimum.

Intrafamily conflict

Different members of the family may come into conflict over social behaviour (Trivers, 1974; Godfray, 1995; Houston et al., 2005; Lessels, 2006) and in ways that are modulated by patterns of dispersal (e.g. Kuijper and Johnston, 2012). Here, we consider the inclusive-fitness interests of the subadult male, his mother and his father, in relation to the optimal levels of belligerence and bravery that he should express. For ease of presentation, for the remainder of our analysis we focus upon a scenario in which there are equal numbers of male and female breeders in each group ($N_{\mathrm{f}} = N_{\mathrm{m}} = N$) and all offspring born in conquered groups are begot by mothers from the conquered group ($s_{\mathrm{f}} = 1$) and by males from the conquering group ($s_{\mathrm{m}} = 0$), and we treat migration rates as fixed parameters (as in Lehmann and Felman (2008); see Extended Methods for more general results and demonstration that all combinations of sex-specific migration rates are evolutionarily feasible). We find that parents always favour a higher level of altruism in warfare than do their sons and that mothers and fathers disagree when there is a sex-bias in migration (Fig. 2.2).

The conditions [2.3] and [2.4] under which increases in belligerence and bravery are favoured depend on relatedness coefficients $R_{\mathrm{male|controller}}$ and $R_{\mathrm{female|controller}}$, which may be different for different controllers. Accordingly, different controllers may have different belligerence (A^*) and bravery (Ω^*) optima. If a male's behaviour is controlled by his father, these relatedness coefficients above are given by $R_{\mathrm{male|father}}$ and $R_{\mathrm{female|father}}$, which may be

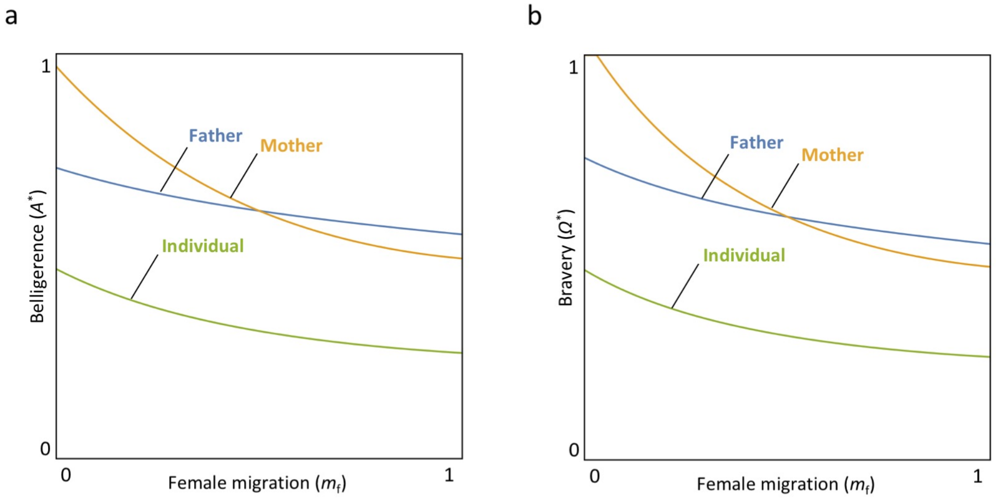

Figure 2.2 - Intrafamily conflicts over belligerence and bravery. Convergence-stable levels of belligerence (A^*, panel a) and bravery (Ω^*, panel b) as a function of female migration (m_{f}) when belligerence is controlled by the focal male's father (blue line), his mother (orange line), and the focal male himself (green line). Other parameter values are $\bar{\omega} = 0.5$ (panel a only), $m_{\mathrm{m}} = 0.5$, $s_{\mathrm{f}} = 1$, $s_{\mathrm{m}} = 0$, $N_{\mathrm{f}} = N_{\mathrm{m}} = 10$. We assume functional forms $a = A_{\mathrm{att}}$ and $t = 1 - 0.05\, a^{1/2}$ (panel a), and $\omega(\Omega_{\mathrm{att}}, \Omega_{\mathrm{def}}) = \Omega_{\mathrm{att}} / (\Omega_{\mathrm{att}} + \Omega_{\mathrm{def}})$ and $\tau = 1 - 0.1\, \Omega^{1/2}$ (panel b).

expressed in terms of model parameters (Table 2.1). Substituting these relatedness coefficients into conditions [2.3] and [2.4], we can determine belligerence (A^*_{father}) and bravery (Ω^*_{father}) optima from the perspective of the subadult male's father, and this recovers the results reported by Lehmann & Feldman (2008, 2009) (see Extended Methods for details; Fig. 2.2). Alternatively, if the male's behaviour is controlled by his mother, relatedness is given by $R_{\text{male|mother}}$ and $R_{\text{female|mother}}$ (Table 2.1). Substituting these relatedness coefficients into conditions [2.3] and [2.4], we can determine belligerence (A^*_{mother}) and bravery (Ω^*_{mother}) optima from the perspective of the subadult male's mother (Fig. 2.2). Finally, if the male's behaviour is under his own, individual control, relatedness is given by $R_{\text{male|individual}}$ and $R_{\text{female|individual}}$ (Table 2.1). Substituting these relatedness coefficients into conditions [2.3] and [2.4], we can determine belligerence ($A^*_{\text{individual}}$) and bravery ($\Omega^*_{\text{individual}}$) optima from the perspective of the subadult male himself (Fig. 2.2).

Table 2.1 - Relatedness. Coefficients of relatedness $R_{\text{recipient|controller}}$ between the controller of a male's behaviour (the individual male himself, his father, his mother, his genes of unknown parental origin, his paternal-origin genes and his maternal-origin genes) and the recipients whose fitnesses are modulated by this behaviour (male groupmates and female groupmates) in the context of belligerence and bravery behaviours. These coefficients depend upon the relatedness of two subadults born in the same group, i.e. $R_x = 2/(4N - (N-1)(1-m_m)^2 - (N-1)\left(1-m_f\right)^2 - 2N\varphi_{MF})$, and the probability that two adults of opposite sex in the same post-competition group were born in the same group, i.e. $\varphi_{MF} = (1 - \bar{a}\bar{\varpi})(1-m_m)(1-m_f)$.

Controller	**Recipient**	
	Male	Female
Individual	$(1-m_{\mathrm{m}})^2 R_{\mathrm{x}}$	$(1-m_{\mathrm{m}})(1-m_{\mathrm{f}})R_{\mathrm{x}}$
Father	$(1-m_{\mathrm{m}})^2\left(\frac{1+N\varphi_{\mathrm{MF}}R_{\mathrm{x}}+(N-1)(1-m_{\mathrm{m}})^2R_{\mathrm{x}}}{N(1+\ \varphi_{\mathrm{MF}}R_{\mathrm{x}})}\right)$	$(1-m_{\mathrm{m}})(1-m_{\mathrm{f}})\left(\frac{1+N\varphi_{\mathrm{MF}}R_{\mathrm{x}}+(N-1)(1-m_{\mathrm{m}})^2R_{\mathrm{x}}}{N(1+\ \varphi_{\mathrm{MF}}R_{\mathrm{x}})}\right)$
Mother	$(1-m_{\mathrm{m}})^2\left(\frac{1+N\varphi_{\mathrm{MF}}R_{\mathrm{x}}+(N-1)(1-m_{\mathrm{f}})^2R_{\mathrm{x}}}{N(1+\ \varphi_{\mathrm{MF}}R_{\mathrm{x}})}\right)$	$(1-m_{\mathrm{m}})(1-m_{\mathrm{f}})\left(\frac{1+N\varphi_{\mathrm{MF}}R_{\mathrm{x}}+(N-1)(1-m_{\mathrm{f}})^2R_{\mathrm{x}}}{N(1+\ \varphi_{\mathrm{MF}}R_{\mathrm{x}})}\right)$
Unknown	$(1-m_{\mathrm{m}})^2 R_{\mathrm{x}}$	$(1-m_{\mathrm{m}})(1-m_{\mathrm{f}})R_{\mathrm{x}}$
Paternal	$(1-m_{\mathrm{m}})^2\left(\frac{1+N\varphi_{\mathrm{MF}}R_{\mathrm{x}}+(N-1)(1-m_{\mathrm{m}})^2R_{\mathrm{x}}}{2N}\right)$	$(1-m_{\mathrm{m}})(1-m_{\mathrm{f}})\left(\frac{1+N\varphi_{\mathrm{MF}}R_{\mathrm{x}}+(N-1)(1-m_{\mathrm{m}})^2R_{\mathrm{x}}}{2N}\right)$
Maternal	$(1-m_{\mathrm{m}})^2\left(\frac{1+N\varphi_{\mathrm{MF}}R_{\mathrm{x}}+(N-1)(1-m_{\mathrm{f}})^2R_{\mathrm{x}}}{2N}\right)$	$(1-m_{\mathrm{m}})(1-m_{\mathrm{f}})\left(\frac{1+N\varphi_{\mathrm{MF}}R_{\mathrm{x}}+(N-1)(1-m_{\mathrm{f}})^2R_{\mathrm{x}}}{2N}\right)$

Comparison of these relatedness coefficients reveals two key results. Firstly, a subadult male is always less related to other subadults in his group than are his parents ($R_{\mathrm{male|individual}} < R_{\mathrm{male|father}}, R_{\mathrm{male|mother}}$; $R_{\mathrm{female|individual}} < R_{\mathrm{female|father}}, R_{\mathrm{female|mother}}$), such that his belligerence and bravery optima are always lower than those of his parents ($A^*_{\mathrm{individual}} < A^*_{\mathrm{father}}, A^*_{\mathrm{mother}}$; $\Omega^*_{\mathrm{individual}} < \Omega^*_{\mathrm{father}}, \Omega^*_{\mathrm{mother}}$; Fig. 2.2). Secondly: the relatedness coefficients from his father's and mother's perspectives coincide only when migration is unbiased ($m_{\mathrm{f}} = m_{\mathrm{m}}$); when migration is female-biased ($m_{\mathrm{f}} > m_{\mathrm{m}}$), his mother is less related than his father to his groupmates ($R_{\mathrm{male|mother}} < R_{\mathrm{male|father}}$; $R_{\mathrm{female|mother}} <$ $< R_{\mathrm{female|father}}$) and, consequently, his mother favours less belligerence and bravery than does his father ($A^*_{\mathrm{mother}} < A^*_{\mathrm{father}}$; $\Omega^*_{\mathrm{mother}} < \Omega^*_{\mathrm{father}}$); and when migration is male-biased ($m_{\mathrm{f}} < m_{\mathrm{m}}$), his mother is more related than his father to his groupmates ($R_{\mathrm{male|mother}} >$ $> R_{\mathrm{male|father}}$; $R_{\mathrm{female|mother}} > R_{\mathrm{female|father}}$) and, consequently, his mother favours more belligerence and bravery than does his father ($A^*_{\mathrm{mother}} > A^*_{\mathrm{father}}$; $\Omega^*_{\mathrm{mother}} > \Omega^*_{\mathrm{father}}$; Fig. 2.2). We confirm the robustness of these analytical results using individual-based simulations (see Extended Methods for details).

Intragenomic conflict

Sex-biased demography has been implicated in intragenomic conflicts for a variety of social behaviours (Haig, 2000; Úbeda and Gardner, 2010; 2011; 2012; Úbeda et al., 2014; Farrell et al., 2015; Van Cleve et al., 2010; Brandvain et al., 2010; Úbeda and Gardner, 2015). Here, we investigate the potential for conflict over belligerence and bravery within the male's genome, by considering the inclusive-fitness interests (Hamilton, 1964; Gardner and Welch, 2011; Gardner, 2014) of his maternal-origin genes, paternal-origin genes and genes of unknown parental origin (Fig. 2.3).

If the male's behaviour were fully controlled by his paternal-origin genes, relatedness coefficients $R_{\text{male|controller}}$ and $R_{\text{female|controller}}$ in conditions [2.3] and [2.4] would be given by $R_{\text{male|paternal}}$ and $R_{\text{female|paternal}}$ (Table 2.1). Substituting these relatedness coefficients into conditions [2.3] and [2.4], we can determine belligerence (A^*_{paternal}) and bravery ($\Omega^*_{\text{paternal}}$) optima from the perspective of the subadult male's paternal-origin genes (Fig. 2.3). Alternatively, if the male's behaviour were fully controlled by his maternal-origin genes, relatedness would be given by $R_{\text{male|maternal}}$ and $R_{\text{female|maternal}}$ (Table 2.1). Substituting these relatedness coefficients into conditions [2.3] and [2.4], we can determine the belligerence (A^*_{maternal}) and bravery ($\Omega^*_{\text{maternal}}$) optima from the perspective of the subadult male's maternal-origin genes (Fig. 2.3). Finally, relatedness for a gene of unknown parental origin is given by $R_{\text{male|unknown}}$ and $R_{\text{female|unknown}}$ (Table 2.1). Notice that these exactly coincide with the relatedness coefficients for the individual carrying the genes, $R_{\text{male|individual}}$ and $R_{\text{female|individual}}$ (Table 2.1). Substituting these relatedness coefficients into conditions [2.3] and [2.4], we can determine belligerence (A^*_{unknown}) and bravery ($\Omega^*_{\text{unknown}}$) optima from the perspective of the subadult male's genes of unknown parental origin (Fig 2.3).

Comparison of relatedness coefficients yields two further key results. Firstly, relatedness for a gene of unknown parental origin is the arithmetic mean of those for maternal-origin and paternal-origin genes (Haig, 1996) and, accordingly, the belligerence or bravery optimum for a gene of unknown parental origin is always intermediate between those of maternal-origin and paternal-origin genes (Fig. 2.3). Secondly: the relatedness coefficients for a male's maternal-origin and paternal-origin genes coincide only when

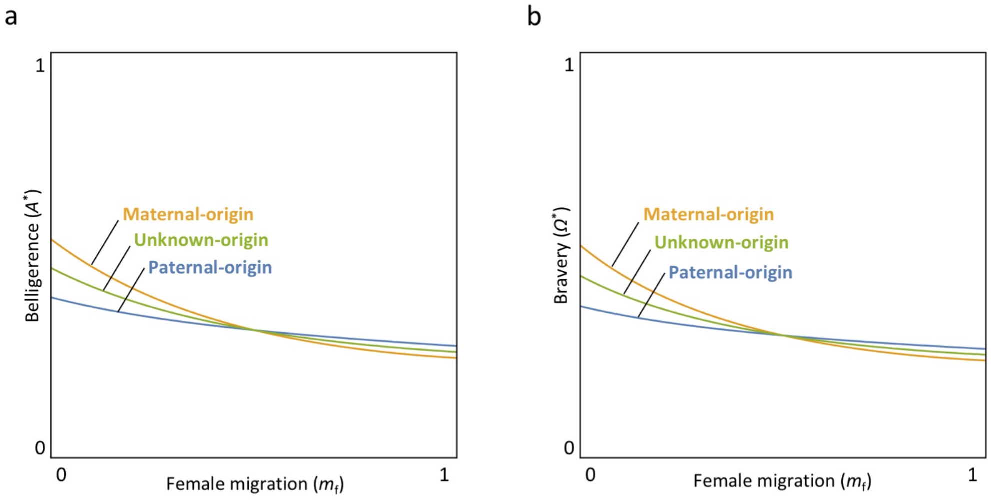

Figure 2.3 - Intragenomic conflicts over belligerence and bravery. Convergence-stable level of belligerence (A^*, panel a) and bravery (Ω^*, panel b) as a function of female migration (m_f) when belligerence or bravery are controlled by the focal individual's paternal-origin genes (blue line), maternal-origin genes (orange line), or unknown-origin genes (green line). Other parameter values are $\bar{\omega} = 0.5$ (panel a only) and $m_\mathrm{m} = 0.5$, $s_\mathrm{f} = 1$, $s_\mathrm{m} = 0$, $N_\mathrm{f} = N_\mathrm{m} = 10$. We assume functional forms $a = A_\mathrm{att}$ and $t = 1 - 0.05\, a^{1/2}$ (panel a), and $\omega(\Omega_\mathrm{att}, \Omega_\mathrm{def}) = \Omega_\mathrm{att} / (\Omega_\mathrm{att} + \Omega_\mathrm{def})$ and $\tau = 1 - 0.1\, \Omega^{1/2}$ (panel b).

migration is unbiased ($m_\mathrm{f} = m_\mathrm{m}$); when migration is female-biased ($m_\mathrm{f} > m_\mathrm{m}$), his maternal-origin genes are less related than his paternal-origin genes to his groupmates ($R_\mathrm{male|maternal} < R_\mathrm{male|paternal}$; $R_\mathrm{female|maternal} < R_\mathrm{female|paternal}$) and, consequently, his maternal-origin genes favour less belligerence and bravery than do his paternal-origin genes ($A^*_\mathrm{maternal} < A^*_\mathrm{paternal}$; $\Omega^*_\mathrm{maternal} < \Omega^*_\mathrm{paternal}$); and when migration is male-biased ($m_\mathrm{f} < m_\mathrm{m}$), his maternal-origin genes are more related than his paternal-origin genes to his groupmates ($R_\mathrm{male|maternal} > R_\mathrm{male|paternal}$; $R_\mathrm{female|maternal} > R_\mathrm{female|paternal}$) and, consequently, his maternal-origin genes favour more belligerence and bravery than do his paternal-origin genes ($A^*_\mathrm{maternal} > A^*_\mathrm{paternal}$; $\Omega^*_\mathrm{maternal} > \Omega^*_\mathrm{paternal}$; Fig. 2.3). We confirm the robustness of these analytical results using individual-based simulations (see Extended Methods for details).

Genomic imprinting

The kinship theory of genomic imprinting suggests that intragenomic conflicts between maternal-origin and paternal-origin genes drive the evolution of parent-of-origin-specific gene expression (Haig, 1996, 2002; Úbeda and Haig, 2003). According to the “loudest voice prevails” principle (Haig, 1996), this conflict ultimately leads to self-imposed silencing of one of the genes. Specifically, if the locus of interest encodes a gene product that promotes the contested phenotype, then the gene with the higher phenotypic optimum is favoured to upregulate its level of expression, while the gene with the lower optimum is favoured to downregulate its expression, and this antagonistic escalation results in the latter gene silencing itself and the former gene expressing at its desired level. In contrast, if the locus encodes a gene product that inhibits the contested phenotype, then it is the gene with the higher phenotypic optimum that is predicted to silence itself and the other gene to express at its desired level.

The loudest-voice-prevails principle may be used to make predictions as to patterns of gene expression for loci underlying belligerence and bravery phenotypes (Fig. 2.4, 2.5). For simplicity, we focus on the case in which relatedness is higher for paternal-origin genes than for maternal-origin genes ($R_{\mathrm{male|paternal}} > R_{\mathrm{male|maternal}}$; $R_{\mathrm{female|paternal}} > R_{\mathrm{female|maternal}}$), e.g. owing to female-biased dispersal. In this scenario, paternal-origin genes favour more belligerence and bravery than do maternal-origin genes ($A^*_{\mathrm{paternal}} > A^*_{\mathrm{maternal}}$; $\Omega^*_{\mathrm{paternal}} > \Omega^*_{\mathrm{maternal}}$). Considering a locus for which the gene product acts to increase belligerence (i.e. a ‘belligerence promoter’), since the maternal-origin gene favours less belligerence than does the paternal-origin gene, we predict the former to be silenced and the latter to be expressed (Fig. 2.4a). In contrast, considering a locus for which the gene product acts to decrease belligerence (i.e. a 'belligerence inhibitor'), we predict the paternal-origin gene to be silenced and the maternal-origin gene to be expressed (Fig. 2.4a). Analogously, we predict that a bravery promoter will be maternally-silenced and paternally-expressed (Fig. 2.4b) and that a belligerence inhibitor will be paternally-silenced and maternally-expressed (Fig. 2.4b). Exactly the opposite patterns are obtained if relatedness is higher for maternal-origin genes than for paternal-origin genes (Fig 2.5).

Associated pathologies

Genomic imprinting results in functional haploidy, rendering the individual vulnerable to a range of deleterious mutations and epimutations (Falls, et al., 1999). These might have no visible effect or, alternatively, lead to abnormal phenotypes and pathological conditions that are very far from realising the inclusive-fitness interests of either maternal-origin or paternal-origin genes (Úbeda and Gardner, 2010). Here, we consider three different types of perturbations: (i) a gene deletion (or, equivalently, a point mutation resulting in a non-functional gene product, or an experimentally-induced knockout); (ii) a malfunctioning of the imprinting machinery, whereby the addition of methyl tags to genes that are normally expressed leads to erroneous silencing ('hyper-methylation'), or the absence of methyl tags from genes that are normally silenced leads to erroneous expression ('hypo-methylation'; Reik and Walter, 2001); and (iii) uniparental disomy, whereby both of the individual's genes derive from one parent. Again, for the purposes of illustration and for compactness of presentation, we only consider only the case of female-biased dispersal in detail.

Considering a belligerence promoter, which is expected to be maternally silenced and paternally expressed: deletion of the maternal-origin gene has no effect and leads to a

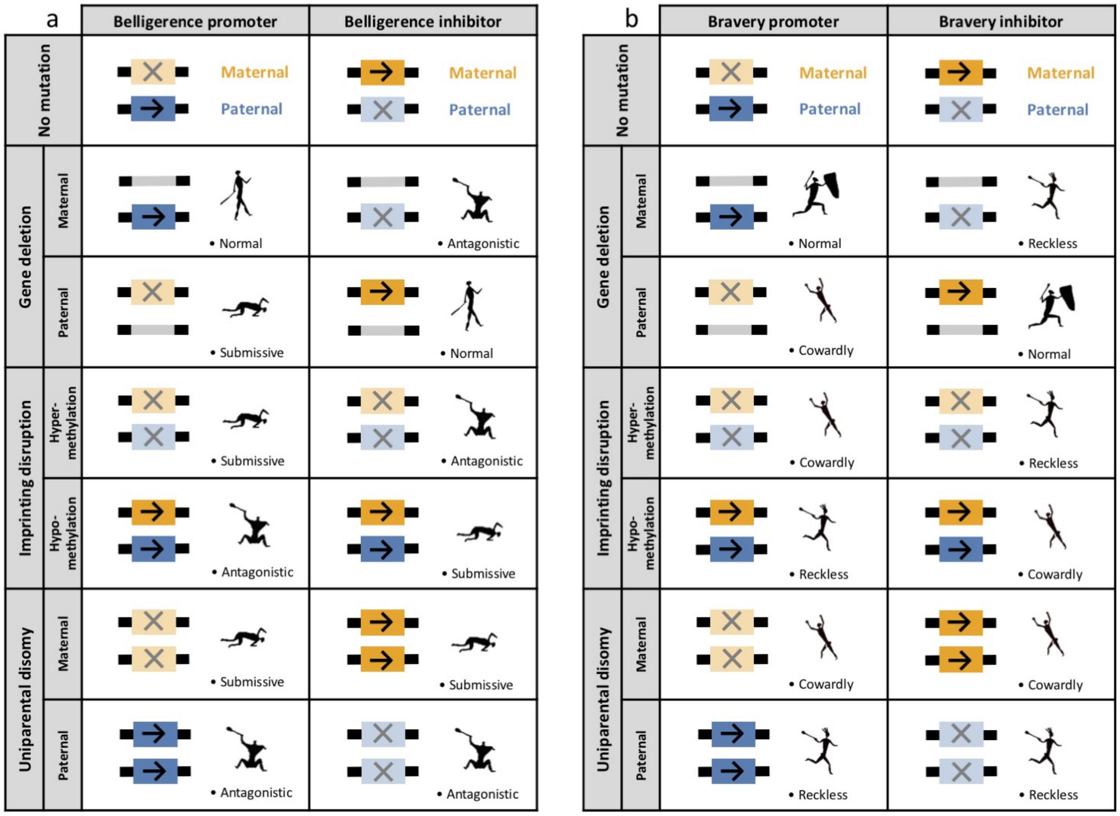

Figure 2.4 - Genomic imprinting and associated pathologies when relatedness is higher for paternal-origin genes than for maternal-origin genes, e.g. under female-biased dispersal. Predicted patterns of parent-of-origin-specific gene expression and concomitant phenotypes for loci that are either promoters or inhibitors of belligerence (panel a) or bravery (panel b), under normal conditions and also as a result of three different mutational or epimutational perturbations: gene deletion, imprinting disruption, uniparental disomy. Genes are either of maternal-origin (orange) or paternal-origin (blue), and are either silenced (crosses) or expressed (arrows). Human figures from the George Stow collection at Iziko South African Museum, derived from The Digital Bleek and Lloyd (http://lloydbleekcollection.cs.uct.ac.za/) with permission.

normal phenotype; deletion of the paternal-origin gene results in the complete absence of gene product and hence an abnormally low level of belligerence (‘submissive’ phenotype); hyper-methylation silences the paternal-origin gene, resulting in the submissive phenotype; hypo-methylation activates the maternal-origin gene, resulting in an ‘antagonistic’ phenotype; maternal disomy results in the complete absence of gene product, and hence the submissive phenotype; and paternal disomy results in an abnormally large amount of gene product, and hence the antagonistic phenotype (Fig. 2.4a). In contrast, considering a belligerence inhibitor, which is expected to be paternally silenced and maternally expressed: deletion of the maternal-origin gene results in the complete absence of gene product and hence the antagonistic phenotype; deletion of the paternal-origin gene results in the normal phenotype; hyper-methylation silences the maternal-origin gene, resulting in the antagonistic phenotype; while hypo-methylation activates the paternal-origin gene, resulting in the submissive phenotype; maternal disomy results in an abnormally high amount of gene product, and hence the submissive phenotype; and paternal disomy results in the complete absence of the gene product, and hence the antagonistic phenotype (Fig. 2.4a). Exactly analogous patterns obtain for bravery genes, with mutations and epimutations variously giving rise to abnormally low levels of bravery (‘cowardly’ phenotype), abnormally high levels of bravery (‘reckless’ phenotype) or a normal phenotype (Fig. 2.4b). Expression patterns for both belligerence and bravery expected under male-biased dispersal – which can be obtained following a rationale analogous to that followed for female-biased dispersal – are illustrated in Fig. 2.5.

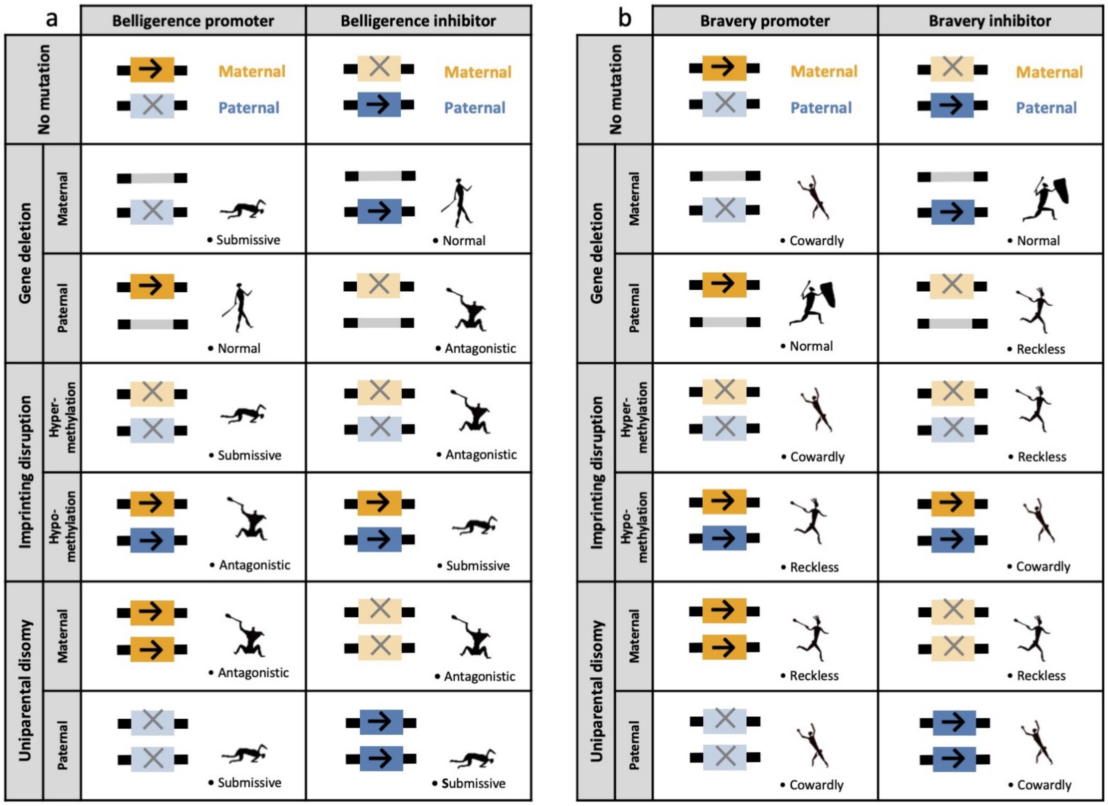

Figure 2.5 - Genomic imprinting and associated pathologies when relatedness is higher for maternal-origin genes than for paternal-origin genes, e.g. under male-biased dispersal. Predicted patterns of parent-of-origin-specific gene expression and concomitant phenotypes for loci that are either promoters or inhibitors of belligerence (panel a) or bravery (panel b), under normal conditions and also as a result of three different mutational or epimutational perturbations: gene deletion, imprinting disruption, uniparental disomy. Genes are either of maternal-origin (orange) or paternal-origin (blue), and are either silenced (crosses) or expressed (arrows). Human figures from the George Stow collection at Iziko South African Museum, derived from The Digital Bleek and Lloyd (http://lloydbleekcollection.cs.uct.ac.za/) with permission.

Discussion

Despite huge interest in the evolution of warfare, conflicts both between family members and within the warring individual have been relatively neglected. Here, we developed and analysed a model of warfare in the context of sex-biased demography. We found that the ecology of war can drive the evolution of sex-biased dispersal. Moreover, we found that these same patterns of sex-biased dispersal can modulate intrafamily and intragenomic conflicts over warfare, and accordingly parent-of-origin-specific patterns of gene expression – i.e. "genomic imprinting" – and concomitant mutational and epimutational pathologies in relation to intergroup violence phenotypes.

We have shown that sex-biased dispersal can be driven by sexual asymmetries in the spoils of war. In particular, insofar as warfare enables males extra opportunities to compete with non-kin for breeding positions – thus relaxing kin competition – to an extent that is greater than for females, then males are less strongly favoured to disperse as means of reducing kin competition for breeding positions (cf. Hamilton and May, 1977; Taylor, 1988) and this may result in the evolution of female-biased dispersal (patrilocality). This ecology-of-war effect provides a novel potential explanation for the unusual female-biased dispersal of ancestral humans (Seielstad, et al., 1998), modern hunter-gatherers (Ember, 1978) and African apes, especially chimpanzees (Lawson Handley and Perrin, 2007), which contrasts with the male-biased dispersal observed in most mammals (Greenwood, 1980; Dobson, 1982). In addition, we have shown that female-biased dispersal may be favoured when females suffer a lower cost of dispersal (cf. Gros, et al., 2008), e.g. owing to a greater likelihood that they will be accepted into a new group, as has been reported in primates (Lawson Handley and Perrin, 2007). Considered together, these two results suggest that male-male violence – in the context of war and/or against immigrants – may have been a key driver of patrilocality.

Our analysis suggests that intense intrafamily conflict may arise in the context of warfare, with parents encouraging reluctant sons to go to war and to show valour in battle (on account of the inclusive-fitness costs of warfare being lower for parents than for sons, it being the latter whose lives are at risk), and with fathers being more encouraging and mothers being more circumspect (on account of the inclusive-fitness benefits of warfare being higher for fathers than for mothers, the former being – on average – more related to the local group). Such conflicts of interests underline the importance of understanding the cultural transmission of warfare (reviewed in Goldschmidt, 1988): in particular, boys learning about war from their fathers – e.g. as occurs in the Jivaro of South America and the Mae Enga of Papua New Guinea (Goldschmidt, 1988) among others – suggests a means by which fathers may exert control over their sons' conduct in relation to warfare. More generally, influence may extend beyond the family, such as when leaders decide the behaviour of their followers (Smith, et al., 2016). These points highlight that genetics and culture need not always provide competing explanations for warfare (*contra* Goldschmidt, 1988; Keeley, 1997), but rather cultural transmission and norms may provide avenues for different genetic parties to exert their influence over human behaviour.

We have also shown that sex-specific demography can generate intragenomic conflict over warfare. Specifically, female-biased dispersal can result in a young male being more related to his groupmates via his father than via his mother, such that his paternal-origin genes are relatively more favoured to induce belligerence and bravery behaviours than are his maternal-origin genes. We predict that this intragenomic conflict will result in genomic imprinting: loci that promote belligerence and/or bravery behaviours are expected to be maternally silenced and paternally expressed, while loci that inhibit these behaviours are expected to be paternally silenced and maternally expressed (Fig. 2.4). Although our main focus has been on female-biased dispersal, other sex-specific demographies are expected to yield similar predictions (cf. Úbeda and Gardner, 2010, 2011, 2012; Úbeda et al., 2014). These include higher male variance in reproductive success (e.g. owing to polygyny; cf. Marlowe, 2005) and higher male mortality (e.g. owing to male-male violence; Gat, 2000a). Importantly, our predictions are expected to be relatively robust to quantitative variation in these sex-specific parameters, as the existence and direction of imprint depends only on the existence and direction – and not the magnitude – of intragenomic conflict (Farrell, et al., 2015).

A remarkable feature of the kinship theory of genomic imprinting is that it not only illuminates adaptation but also yields testable predictions as to the particular maladaptive phenotypes associated with deleterious genetic and epigenetic mutations (Haig and Wharton, 2003; Crespi and Badcock, 2008; Úbeda and Wilkins, 2008; Úbeda and Gardner, 2010, 2011, 2015; Úbeda et al., 2014). We have shown that mutations and epimutations tilting the balance towards paternally-expressed belligerence and bravery loci are expected to result in 'aggressive' and 'reckless' pathologies, while those tilting the balance towards maternally-expressed loci are expected to result in 'submissive' and 'cowardly' pathologies, these being extreme phenotypes that lie far beyond the inclusive-fitness optima of any of the individual's genes. Accordingly, our analysis suggests that some instances of societally damaging intergroup violence may represent maladaptive defects rather than well-honed adaptations to our ancestral environment. Understanding that such violence may be associated with imprinting disorders should facilitate discovery of the genes involved.

Extended Methods

Fitness

We begin by deriving the fitness of a focal subadult male in a focal group. We consider fitness under all possible dispersal decisions, events and outcomes of war, following the life cycle described in Methods and represented in Figure A2.1. With probability $1 - d_{\mathrm{m}}$, the focal male does not disperse and remains in the focal group. In every generation, each post-dispersal group is in a position to attack one randomly-chosen group and to be attacked by one other group. The focal group is not attacked by the other group with probability $1 - \bar{a}$, in which case the focal male competes for N_{m} breeding spots with $N_{\mathrm{f}} K_{\mathrm{m}}((1 - d'_{\mathrm{m}}) + \bar{d}_{\mathrm{m}} (1 - \lambda_{\mathrm{m}}))\, t(A')$ males, where $t(A')$ is the group-average competitiveness (with $\mathrm{d}t/\mathrm{d}A < 0$, and $t(0) = 1$). Considering that the competitiveness of the focal male due to belligerence is $t(A)$, his probability of securing a breeding spot in this case is $(N_{\mathrm{m}}\, t(A))/(N_{\mathrm{f}} K_{\mathrm{m}}((1 - d'_{\mathrm{m}}) + \bar{d}_{\mathrm{m}} (1 - \lambda_{\mathrm{m}}))\, t(A'))$. Alternatively, the focal group is attacked with probability $\bar{a}$ and the attacking group loses the war with probability $1 - \omega''$, where $\omega'' \equiv \omega(\bar{\Omega}, \Omega')$. In this case, the probability of survival of the average male in the group is multiplied by $\tau(\Omega')$ and that of the focal male by $\tau(\Omega)$, where $\tau(\Omega_{\mathrm{ind}})$ is competitiveness due to bravery (with $\mathrm{d}\tau/\mathrm{d}\,\Omega < 0$, and $\tau(0) = 1$). Therefore, in this case, the focal male secures a breeding spot with probability $(N_{\mathrm{m}}\, t(A)\, \tau(\Omega))/(N_{\mathrm{f}} K_{\mathrm{m}}((1 - d'_{\mathrm{m}}) + \bar{d}_{\mathrm{m}} (1 - \lambda_{\mathrm{m}}))\, t(A')\, \tau(\Omega'))$. We assume that the competitiveness terms due to belligerence and bravery are multiplicative for mathematical convenience. Otherwise, the attacking group wins the war with probability ω'' and in this case the focal male competes for $N_{\mathrm{m}}\, s_{\mathrm{m}}$ breeding spots with $N_{\mathrm{f}} K_{\mathrm{m}}((1 - d'_{\mathrm{m}}) + \bar{d}_{\mathrm{m}} (1 - \lambda_{\mathrm{m}}))\, s_{\mathrm{m}}$ males from his group and $N_{\mathrm{f}} K_{\mathrm{m}}((1 - \bar{d}_{\mathrm{m}}) + \bar{d}_{\mathrm{m}} (1 - \lambda_{\mathrm{m}}))\,(1 - s_{\mathrm{m}})$ males from the attacking group. Adding the appropriate competitiveness modifiers, the overall probability that the focal male secures a spot in this case is $(N_{\mathrm{m}}\, t(A)\, \tau(\Omega)\, s_{\mathrm{m}}) / (N_{\mathrm{f}} K_{\mathrm{m}}((1 - d'_{\mathrm{m}}) + \bar{d}_{\mathrm{m}} (1$

$-\lambda_\mathrm{m})) \, t(A') \, \tau(\Omega') \, s_\mathrm{m} + N_\mathrm{f} K_\mathrm{m} ((1 - \bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m} (1 - \lambda_\mathrm{m})) \, t(\bar{A}) \, \tau(\bar{\Omega})) \, (1 - s_\mathrm{m}))$. In addition, the focal group has the opportunity to attack one other group. With probability $1 - a'$, where $a' = a(A')$, this does not happen, and in this case the focal male does not get access to additional breeding spots. Alternatively, the focal group goes to war with probability a' and loses with probability $1 - \omega'$, where $\omega' = \omega(\Omega', \bar{\Omega})$, which again results in no additional breeding spots for the focal male. Otherwise, the focal group wins with probability ω' in which case the focal male has access to an additional $N_\mathrm{m} (1 - s_\mathrm{m})$ breeding spots, for which he competes with $N_\mathrm{f} K_\mathrm{m} ((1 - d'_\mathrm{m}) + \bar{d}_\mathrm{m} (1 - \lambda_\mathrm{m}))(1 - s_\mathrm{m})$ males from his group and $N_\mathrm{f} K_\mathrm{m}((1 - \bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m} (1 - \lambda_\mathrm{m})) \, s_\mathrm{m}$ males from the conquered group. Taking into account the competitiveness due to belligerence and bravery as before, the probability that the focal male secures a breeding spot in this case is equal to $(N_\mathrm{m} \, t(A) \, \tau(\Omega) \, (1 - s_\mathrm{m})) \, / \, (N_\mathrm{f} K_\mathrm{m} ((1 - d'_\mathrm{m}) + \bar{d}_\mathrm{m} (1 - \lambda_\mathrm{m})) \, t(A') \, \tau(\Omega') \, (1 - s_\mathrm{m}) + N_\mathrm{f} K_\mathrm{m} ((1 - \bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m} (1 - \lambda_\mathrm{m})) \, t(\bar{A}) \, \tau(\bar{\Omega}) \, s_\mathrm{m})$. Alternatively, the focal male disperses from the natal group with probability d_m and successfully reaches and becomes part of another group with probability $1 - \lambda_\mathrm{m}$. In this case, fitness is derived analogously to the philopatry case, with the exception that the number of males in the focal group is equal to $N_\mathrm{f} K_\mathrm{m} ((1 - \bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m} (1 - \lambda_\mathrm{m}))$. Therefore, the absolute fitness of a focal subadult male is equal to:

$$
\begin{aligned}
w_\mathrm{m} = \Bigg(& (1 - d_\mathrm{m}) \Bigg((1 - \bar{a}) \frac{t(A)}{\big((1-d'_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})\big) t(A')} + \bar{a} \Bigg((1 - \omega'') \frac{t(A) \, \tau(\Omega)}{\big((1-d'_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})\big) t(A') \tau(\Omega')} + \\
& \omega'' \frac{t(A) \tau(\Omega) s_\mathrm{m}}{\big((1-d'_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})\big) t(A') \tau(\Omega') s_\mathrm{m} + \big((1-\bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})\big) t(\bar{A}) \, \tau(\bar{\Omega})(1-s_\mathrm{m})} \Bigg) + \\
& a' \, \omega' \frac{t(A) \, \tau(\Omega)(1-s_\mathrm{m})}{\big((1-d'_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})\big) t(A') \tau(\Omega')(1-s_\mathrm{m}) + \big((1-\bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})\big) t(\bar{A}) \, \tau(\bar{\Omega}) s_\mathrm{m}} \Bigg) + d_\mathrm{m}(1 - \lambda_\mathrm{m}) \Bigg((1 - \\
& \bar{a}) \frac{t(A)}{t(A')} \frac{1}{(1-\bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})} + \bar{a} \Bigg((1 - \omega'') \frac{t(A) \, \tau(\Omega)}{t(A') \tau(\Omega')} \frac{1}{(1-\bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})} + \\
& \omega'' \frac{t(A) \, \tau(\Omega) s_\mathrm{m}}{((1-\bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})) t(A') \tau(\Omega') s_\mathrm{m} + \big((1-\bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})\big) t(\bar{A}) \, \tau(\bar{\Omega})(1-s_\mathrm{m})} \Bigg) + \\
& \bar{a} \bar{\omega} \frac{t(A) \, \tau(\Omega)(1-s_\mathrm{m})}{((1-\bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})) t(A') \tau(\Omega')(1-s_\mathrm{m}) + \big((1-\bar{d}_\mathrm{m}) + \bar{d}_\mathrm{m}(1-\lambda_\mathrm{m})\big) \, t(\bar{A}) \, \tau(\bar{\Omega}) s_\mathrm{m}} \Bigg) \Bigg) \frac{N_\mathrm{m}}{N_\mathrm{f} K_\mathrm{m}}.
\end{aligned}
\qquad \text{[A2.1]}
$$

The average fitness of subadult males in the population is $\overline{w}_{\mathrm{m}} = N_{\mathrm{m}}/(K_{\mathrm{m}}\, N_{\mathrm{f}})$. Therefore, the relative fitness of the focal subadult male is given by $W_{\mathrm{m}} = w_{\mathrm{m}} / \overline{w}_{\mathrm{m}}$. Similarly, the absolute fitness of a focal subadult female can be written as:

$$w_{\mathrm{f}} = \Bigg((1-d_{\mathrm{f}}) \Bigg((1-\bar{a}) \frac{1}{(1-d'_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})} + \bar{a} \Bigg((1-\omega'') \frac{1}{(1-d'_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})} +$$

$$\omega'' \frac{s_{\mathrm{f}}}{\big((1-d'_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})\big)s_{\mathrm{f}}+\big((1-\bar{d}_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})\big)(1-s_{\mathrm{f}})} \Bigg) + a'\,\omega' \frac{(1-s_{\mathrm{f}})}{\big((1-d'_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})\big)(1-s_{\mathrm{f}})+\big((1-\bar{d}_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})\big)s_{\mathrm{f}}} \Bigg) +$$

$$d_{\mathrm{f}}(1-\lambda_{\mathrm{f}}) \Bigg((1-\bar{a}) \frac{1}{(1-\bar{d}_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})} + \bar{a} \Bigg((1-\omega'') \frac{1}{(1-\bar{d}_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})} +$$

$$\omega'' \frac{s_{\mathrm{f}}}{\big((1-\bar{d}_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})\big)s_{\mathrm{f}}+\big((1-\bar{d}_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})\big)(1-s_{\mathrm{f}})} \Bigg) + \bar{a}\overline{\omega} \frac{(1-s_{\mathrm{f}})}{\big((1-\bar{d}_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})\big)(1-s_{\mathrm{f}})+\big((1-\bar{d}_{\mathrm{f}})+\bar{d}_{\mathrm{f}}(1-\lambda_{\mathrm{f}})\big)s_{\mathrm{f}}} \Bigg) \Bigg) \frac{1}{K_{\mathrm{f}}}\,.$$

[A2.2]

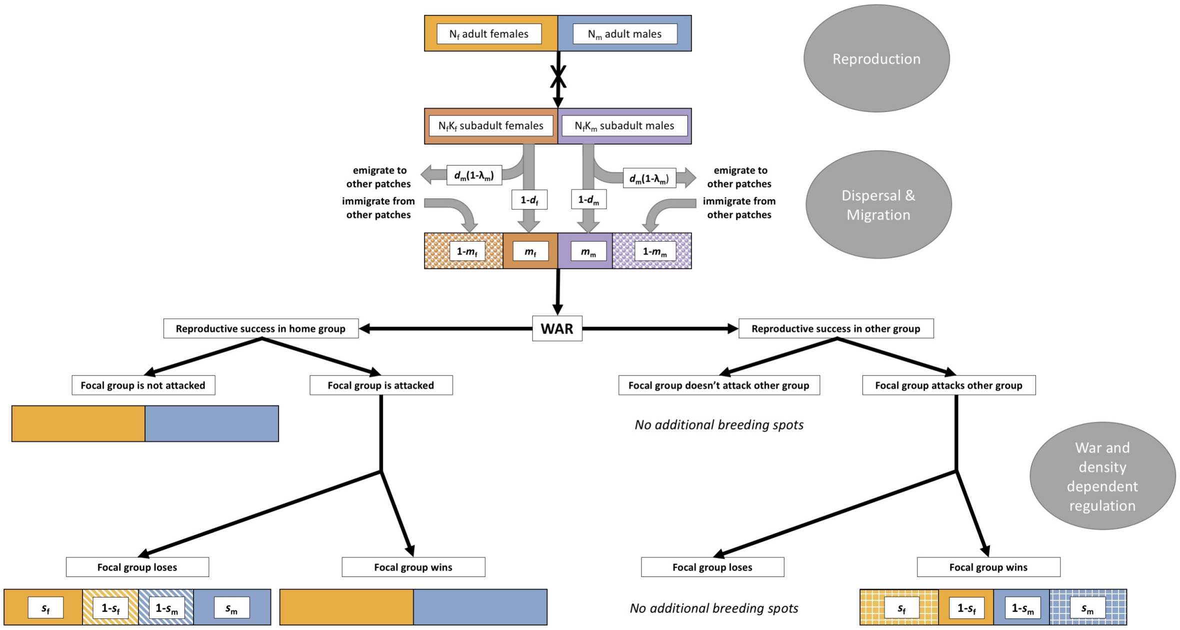

Figure A2.1 – Life cycle as described in the Methods section. Orange and blue represent adult males and females, respectively; brown and purple represent subadult females and males, respectively.

Notice that females do not express the genes for belligerence and bravery and therefore do not pay the associated costs. The average fitness of subadult females in the population is $\bar{w}_\mathrm{f} = 1/K_\mathrm{f}$. Therefore, the relative fitness of the focal subadult female is given by $W_\mathrm{f} = w_\mathrm{f} / \bar{w}_\mathrm{f}$.

Female dispersal

MARGINAL FITNESS

Consider a locus $\mathcal{G}$. We denote the genic value of the focal individual for this gene by g. Secondly, we denote the breeding value of the individual controlling the phenotype (the 'controller') by G, that of a groupmate's controller by G', and the average of the population by $\bar{G}$. Note that, in the case in which the controller is the focal individual, G is the breeding value of the focal individual. Consider that this locus controls female dispersal (the phenotype is exhibited by females, but not by males). Assuming vanishing genetic variation, meaning that all breeding values of the population are clustered around the mean (Taylor, 1996; Taylor and Frank 1996), the direction of natural selection is given by:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_\mathrm{f}\frac{\mathrm{d}W_\mathrm{f}}{\mathrm{d}g_\mathrm{f}} + c_\mathrm{m}\frac{\mathrm{d}W_\mathrm{m}}{\mathrm{d}g_\mathrm{m}}, \qquad \text{[A2.3]}$$

where: $W = c_\mathrm{f}\, W_\mathrm{f} + c_\mathrm{m}\, W_\mathrm{m}$ is an average of relative fitness, taken over female and male classes, with the class reproductive values c_f and c_m of females and males providing the appropriate weights (Fisher, 1930; Price and Smith, 1972; Taylor and Frank, 1996; Frank, 1997; Taylor, et al., 2007); and with all derivatives evaluated at $g = g_\mathrm{m} = g_\mathrm{f} = \bar{G}$.

The derivative $\mathrm{d}W_\mathrm{f}/\mathrm{d}g_\mathrm{f}$ describes how the genic value of a gene drawn from a subadult female impacts on her relative fitness. It depends on i) the association between the dispersal phenotype of the focal female and her own relative fitness, the association between the breeding value for the dispersal gene of the female's controller and the focal female's dispersal phenotype, the association between the genic value of the focal female and the breeding value of her controller, and ii) the association between the dispersal phenotype of a random female in the focal group and the focal female's relative fitness, the association between the breeding value for the dispersal gene of the random female's controller and the random female's dispersal phenotype, the association between the genic value of the focal female and the breeding value of the random female's controller. This can be expressed mathematically as:

$$\frac{\mathrm{d}W_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} = \frac{\partial W_{\mathrm{f}}}{\partial d_{\mathrm{f}}}\frac{\mathrm{d}d_{\mathrm{f}}}{\mathrm{d}G}\frac{\mathrm{d}G}{\mathrm{d}g_{\mathrm{f}}} + \frac{\partial W_{\mathrm{f}}}{\partial d_{\mathrm{f}'}}\frac{\mathrm{d}d_{\mathrm{f}'}}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_{\mathrm{f}}} = \left(\frac{\partial W_{\mathrm{f}}}{\partial d_{\mathrm{f}}} p_{\mathrm{controller}} + \frac{\partial W_{\mathrm{f}}}{\partial d_{\mathrm{f}'}} p_{\mathrm{female}}\right)\gamma\ , \qquad \text{[A2.4]}$$

where $p_{\mathrm{controller}} = \mathrm{d}G/\mathrm{d}g_{\mathrm{f}}$ is the consanguinity between the focal female and her controller, $p_{\mathrm{female}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{f}}$ is the consanguinity between the controller of the focal female and a random female in the focal female's group, and $\gamma = \mathrm{d}d_{\mathrm{f}}/\mathrm{d}G = \mathrm{d}d_{\mathrm{f}}'/\mathrm{d}G'$ is the correlation between an individual's phenotype and its controller's breeding value.

The derivative $\mathrm{d}W_{\mathrm{m}}/\mathrm{d}g_{\mathrm{m}}$ describes how the genic value of a gene drawn from a subadult male impacts on his relative fitness. Since males carry the gene, but do not express it, and competition occurs within sexes, there is no impact on male fitness and this derivative is null.

The condition for an increase in population average female dispersal is $\mathrm{d}W/\mathrm{d}g > 0$ (Taylor, 1996) and, as $c_{\mathrm{f}} = c_{\mathrm{m}} = 1/2$ under diploid inheritance (Taylor, 1996; Fisher, 1930; Price and Smith 1972), this condition is equivalent to:

$$-\frac{\lambda_{\mathrm{f}}}{1-\bar{d}_{\mathrm{f}}\,\lambda_{\mathrm{f}}} p_{\mathrm{controller}} + \frac{(1-\bar{d}_{\mathrm{f}})\left(1-2\bar{a}\bar{\omega}s_{\mathrm{f}}(1-s_{\mathrm{f}})\right)}{(1-\bar{d}_{\mathrm{f}}\,\lambda_{\mathrm{f}})^2} p_{\mathrm{female}} > 0. \qquad \text{[A2.5]}$$

Substituting $p_{\mathrm{controller}}$ and p_{female} in [A2.5] with with p_{I} and p_{x} (see CONSANGUINITY AND RELATEDNESS below) and dividing by p_{I} to obtain r_{female}, yields the condition for increase of the male dispersal gene when the focal male controls his phenotype (condition [2.1] in Results).

CONSANGUINITY AND RELATEDNESS

The coefficient of consanguinity $p_{\mathrm{A,B}}$ between two individuals A and B is defined as the probability that a gene drawn at random from a given locus in individual A is identical-by-descent to a gene drawn at random from the same locus in individual B (Bulmer, 1994). The second individual may coincide with the first (B=A), in which case we obtain the consanguinity of an individual to itself $p_{\mathrm{A,A}}$. In particular, the consanguinity of a diploid individual to itself is $p_{\mathrm{I}} = (1 + f\,)/2$, where f is the inbreeding coefficient. This is the consanguinity between individuals of opposite sex (mating partners) in a post-competition group and is given by $f = \varphi_{\mathrm{MF}}\, p_{\mathrm{x}}$, where $\varphi_{\mathrm{MF}} = (1 - \bar{a}\ \bar{\omega}\ (2 s_{\mathrm{m}} s_{\mathrm{f}} - s_{\mathrm{f}} - s_{\mathrm{m}})(1 - m_{\mathrm{f}})\ (1 - m_{\mathrm{m}})$ expresses the probability that two adults of opposite sex in the same post-competition group were born in the same group. Analogously, the consanguinities of two adult females and two adult males in a post-competition group are $p_{FF} = \varphi_{\mathrm{FF}}\, p_{\mathrm{x}}$ and $p_{MM} = \varphi_{\mathrm{MM}}\, p_{\mathrm{x}}$, where $\varphi_{\mathrm{FF}} = (1 - 2\ \bar{a}\ \bar{\omega}\ s_{\mathrm{f}}(1 - s_{\mathrm{f}}))(1 - m_{\mathrm{f}})^2$ and $\varphi_{\mathrm{MM}} = (1 - 2\ \bar{a}\ \bar{\omega}\ s_{\mathrm{m}}(1 - s_{\mathrm{m}}))(1 - m_{\mathrm{m}})^2$ express the probability that two adult females and two adult males, respectively, in the same post-competition group were born in the same group. p_{x} is the consanguinity of individuals born in the same group and is equal to:

$$p_{\mathrm{x}} = \frac{1}{4}\left(\frac{1}{N_{\mathrm{m}}} p_{\mathrm{I}} + \frac{N_{\mathrm{m}}-1}{N_{\mathrm{m}}} p_{\mathrm{MM}}\right) + \frac{1}{2} f + \frac{1}{4}\left(\frac{1}{N_{\mathrm{f}}} p_{\mathrm{I}} + \frac{N_{\mathrm{f}}-1}{N_{\mathrm{f}}} p_{\mathrm{FF}}\right). \qquad [\text{A2.6}]$$

Substituting the appropriate consanguinities in the equation above and solving for p_x, an expression only dependent on demographic parameters is obtained:

$$p_{\mathrm{x}} = \frac{(N_{\mathrm{f}}+N_{\mathrm{m}})\ \varphi_{\mathrm{MF}}}{8\ N_{\mathrm{f}}\ N_{\mathrm{m}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\ \varphi_{\mathrm{MM}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\ \varphi_{\mathrm{FF}} - (4N_{\mathrm{f}}\ N_{\mathrm{m}} + N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{MF}}}. \qquad [\text{A2.7}]$$

The coefficient of relatedness $r_{\mathrm{A,B}}$ between two individuals A and B is defined as the ratio of the consanguinity of individual B to individual A, $p_{\mathrm{A,B}}$, and the consanguinity of individual B to herself, $p_{\mathrm{B,B}}$ (Bulmer, 1994). The relatedness between a focal subadult female and a random female in her group is given by $r_{\mathrm{female}} = p_{\mathrm{x}}/p_{\mathrm{I}}$, and coincides with the relatedness between a focal subadult male in his group, r_{male} (see conditions [1.1-1.2]). In explicit form:

$$r_{\text{female}} = r_{\text{male}} = \frac{2(N_\text{f}+N_\text{m})}{8N_\text{f}N_\text{m}-2N_\text{f}(N_\text{m}-1)\varphi_{\text{MM}}-2N_\text{m}(N_\text{f}-1)\varphi_{\text{FF}}-4N_\text{f}N_\text{m}\varphi_{\text{MF}}}. \qquad [\text{A2.8}]$$

Male dispersal

MARGINAL FITNESS

Now, consider that the locus G controls male dispersal (the phenotype is exhibited by males, but not by females). Assuming vanishing genetic variation, the direction of natural selection is given by equation [A2.3] with all derivatives evaluated at $g = g_\text{m} = g_\text{f} = \bar{G}$.

The derivative $\text{d}W_\text{f}/\text{d}g_\text{f}$ (in equation [A2.3]) describes how the genic value of a gene drawn from a subadult female impacts on her relative fitness. Since females carry the gene, but do not express it, and competition occurs within sexes, there is no impact on female fitness and this derivative is null.

The derivative $\text{d}W_\text{m}/\text{d}g_\text{m}$ (in equation [A2.3]) describes how the genic value of a gene drawn from a subadult male impacts on his relative fitness. It depends on i) the association between the dispersal phenotype of the focal male and his own relative fitness, the association between the breeding value for the dispersal gene of the male's controller and the focal male's dispersal phenotype, the association between the genic value of the focal male and the breeding value of his controller, and ii) the association between the dispersal phenotype of a random male in the focal group and the focal male's relative fitness, the association between the breeding value for the dispersal gene of the random male's controller and the random male's dispersal phenotype, the association between the genic value of the focal male and the breeding value of the random male's controller. This can be expressed mathematically:

$$\frac{\text{d}W_\text{m}}{\text{d}g_\text{m}} = \frac{\partial W_\text{m}}{\partial d_\text{m}}\frac{\text{d}d_\text{m}}{\text{d}G}\frac{\text{d}G}{\text{d}g_\text{m}} + \frac{\partial W_\text{m}}{\partial d_{\text{m}'}}\frac{\text{d}d_{\text{m}'}}{\text{d}G'}\frac{\text{d}G'}{\text{d}g_\text{m}} = \left(\frac{\partial W_\text{m}}{\partial d_\text{m}}p_{\text{controller}} + \frac{\partial W_\text{m}}{\partial d_{\text{m}'}}p_{\text{male}}\right)\gamma\ , \qquad [\text{A2.9}]$$

where $p_{\mathrm{controller}} = \mathrm{d}G/\mathrm{d}g_{\mathrm{m}}$ is the consanguinity between the focal male and his controller, and $p_{\mathrm{male}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{m}}$ is the consanguinity between the controller of the focal male and a random male in the focal male's group.

The condition for an increase in population average female dispersal is $\mathrm{d}W/\mathrm{d}g > 0$ and, as $c_{\mathrm{f}} = c_{\mathrm{m}} = 1/2$ under diploid inheritance, this condition is equivalent to:

$$-\frac{\lambda_{\mathrm{m}}}{1-\bar{d}_{\mathrm{m}}\,\lambda_{\mathrm{m}}}p_{\mathrm{controller}} + \frac{(1-\bar{d}_{\mathrm{m}})\big(1-2\bar{a}\bar{\omega}s_{\mathrm{m}}(1-s_{\mathrm{m}})\big)}{(1-\bar{d}_{\mathrm{m}}\,\lambda_{\mathrm{m}})^2}p_{\mathrm{male}} > 0. \qquad \text{[A2.10]}$$

Substituting $p_{\mathrm{controller}}$ and p_{male} in [A2.10] with with p_{I} and p_{x} (see CONSANGUINITY AND RELATEDNESS) and dividing by p_{I} to obtain r_{male}, yields the condition for increase of the male dispersal gene when the focal male controls his phenotype (condition [2.2] in Results).

Sex-biased dispersal and migration

CONDITIONS FOR SEX-BIASED DISPERSAL

Here we demonstrate that $M_{\mathrm{f}} < M_{\mathrm{m}}$ is a sufficient condition for $m_{\mathrm{f}}^* \geq m_{\mathrm{m}}^*$ and that $M_{\mathrm{f}} > M_{\mathrm{m}}$ is a sufficient condition for $m_{\mathrm{f}}^* \leq m_{\mathrm{m}}^*$, when $\lambda_{\mathrm{f}} = \lambda_{\mathrm{m}} = \lambda$; that is, when the costs of dispersal are equal for the two sexes, greater paternal admixture results in female migration being greater than or equal to male migration, and greater maternal admixture results in male migration being greater than or equal to female migration. Under this assumption and considering that $r_{\mathrm{female}} = r_{\mathrm{male}} = r$, the marginal fitness function for female dispersal is $\theta_{\mathrm{f}} = -\lambda + (1 - 2\bar{a}\bar{\omega}M_{\mathrm{f}})(1 - m_{\mathrm{f}})\,r$ and the marginal fitness function for male dispersal is $\theta_{\mathrm{m}} = -\lambda + (1 - 2\bar{a}\bar{\omega}M_{\mathrm{m}})(1 - m_{\mathrm{m}})\,r$. Each migration term can assume either boundary (0 and 1) or intermediate values. Therefore, nine cases are possible. We consider them in turn:

i) $m_{\mathrm{f}}^* = 0$ and $m_{\mathrm{m}}^* = 0$; then $\theta_{\mathrm{f}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} \leq 0$ and $\theta_{\mathrm{m}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} = 0$, which requires $M_{\mathrm{f}} \geq (\mathrm{r} - \lambda)/(2\ \bar{a}\ \bar{\omega}\,r)$ and $M_{\mathrm{m}} \geq (\mathrm{r} - \lambda)/(2\ \bar{a}\ \bar{\omega}\,r)$. Therefore: it is sufficient to have $M_{\mathrm{f}} > M_{\mathrm{m}}$ or $M_{\mathrm{f}} < M_{\mathrm{m}}$ for $m_{\mathrm{f}}^* = m_{\mathrm{m}}^* = 0$.

ii) $m_f^* = 0$ and $0 < m_m^* < 1$; then $\theta_f|_{m_f=m_f^*, m_m=m_m^*} \leq 0$ and $\theta_m|_{m_f=m_f^*, m_m=m_m^*} = 0$, which requires $M_f \geq (r - \lambda)/(2\ \bar{a}\ \bar{\omega}\, r)$ and $M_m < (r - \lambda)/(2\ \bar{a}\ \bar{\omega}\, r)$. Therefore: $M_f > M_m$.

iii) $m_f^* = 0$ and $m_m^* = 1$; then $\theta_m|_{m_f=m_f^*, m_m=m_m^*} \geq 0$, which results in $-\lambda \geq 0$. This contradicts our assumption that $\lambda > 0$ and therefore this case is impossible.

iv) $0 < m_f^* < 1$ and $m_m^* = 0$; then $\theta_f|_{m_f=m_f^*, m_m=m_m^*} = 0$ and $\theta_m|_{m_f=m_f^*, m_m=m_m^*} \leq 0$, which requires $M_f < (r - \lambda)/(2\ \bar{a}\ \bar{\omega}\, r)$ and $M_m \geq (r - \lambda)/(2\ \bar{a}\ \bar{\omega}\, r)$. Therefore: $M_f < M_m$.

v) $0 < m_f^* < 1$ and $0 < m_m^* < 1$; then $\theta_f|_{m_f=m_f^*, m_m=m_m^*} = 0$ and $\theta_m|_{m_f=m_f^*, m_m=m_m^*} = 0$, which requires $m_f^* = 1 - \lambda/(1 - 2\ \bar{a}\ \bar{\omega}\, M_f)r$ and $m_m^* = 1 - \lambda/(1 - 2\ \bar{a}\ \bar{\omega}\, M_m)r$. Therefore: $m_f^* > m_m^*$ if and only if $M_f < M_m$ and $m_f^* < m_m^*$ if and only if $M_f > M_m$.

vi) $0 < m_f^* < 1$ and $m_m^* = 1$; this case is impossible (see case iii)).

vii) $m_f^* = 1$ and $m_m^* = 0$; then $\theta_m|_{m_f=m_f^*, m_m=m_m^*} \geq 0$, which results in $-\lambda \geq 0$. This contradicts our assumption that $0 < \lambda \leq 1$ and therefore this case is impossible.

viii) $m_f^* = 1$ and $0 < m_m^* < 1$; this case is impossible (see case vii)).

ix) $m_f^* = 1$ and $m_m^* = 1$; this case is impossible (see case vii)).

As $M_f < M_m$ obtains in every scenario in which $m_f^* \geq m_m^*$, and as $M_f > M_m$ obtains in every scenario in which $m_f^* \leq m_m^*$, we have demonstrated that $M_f < M_m$ is a sufficient condition for $m_f^* \geq m_m^*$ and $M_f \geq M_m$ is a sufficient condition for $m_f^* \leq m_m^*$, when $\lambda_f = \lambda_m = \lambda$.

Noting that:

$$m_f \geq m_m \Rightarrow \frac{d_f(1-\lambda)}{1-d_f\lambda} \geq \frac{d_m(1-\lambda)}{1-d_m\lambda} \Rightarrow d_f \geq d_m, \qquad \text{[A2.11]}$$

and

$$m_{\mathrm{f}} \le m_{\mathrm{m}} \Longrightarrow \frac{d_{\mathrm{f}}(1-\lambda)}{1-d_{\mathrm{f}}\lambda} \le \frac{d_{\mathrm{m}}(1-\lambda)}{1-d_{\mathrm{m}}\lambda} \Longrightarrow\ d_{\mathrm{f}} \le d_{\mathrm{m}}, \qquad \text{[A2.12]}$$

it is also true that that $M_{\mathrm{f}} < M_{\mathrm{m}}$ is a sufficient condition for $d_{\mathrm{f}}^* \ge d_{\mathrm{m}}^*$ and that $M_{\mathrm{f}} > M_{\mathrm{m}}$ is a sufficient condition for $d_{\mathrm{f}}^* \le d_{\mathrm{m}}^*$, when $\lambda_{\mathrm{f}} = \lambda_{\mathrm{m}} = \lambda$.

Secondly, we demonstrate that $\lambda_{\mathrm{f}} < \lambda_{\mathrm{m}}$ is a sufficient condition for $m_{\mathrm{f}}^* \ge m_{\mathrm{m}}^*$ and that $\lambda_{\mathrm{f}} > \lambda_{\mathrm{m}}$ is a sufficient condition for $m_{\mathrm{f}}^* \le m_{\mathrm{m}}^*$, when $M_{\mathrm{f}} = M_{\mathrm{m}} = M$; that is, when maternal and paternal admixture are equal, greater cost of male dispersal results in female migration being greater or equal to male migration, and greater cost of female dispersal results in male migration being greater or equal to female migration. Under this assumption the marginal fitness function for female dispersal is $\theta_{\mathrm{f}} = -\lambda_{\mathrm{f}} + (1-2\bar{a}\bar{\omega}M)(1-m_{\mathrm{f}})\, r$ and the marginal fitness function for male dispersal is $\theta_{\mathrm{m}} = -\lambda_{\mathrm{m}} + (1-2\bar{a}\bar{\omega}M)(1-m_{\mathrm{m}})\, r$. We consider all possible cases. Analogously to the previous demonstration, cases iii), vi), vii), viii), and ix) lead to a contradiction. We consider the remaining cases:

i) $m_{\mathrm{f}}^* = 0$ and $m_{\mathrm{m}}^* = 0$; then $\theta_{\mathrm{f}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} \le 0$ and $\theta_{\mathrm{m}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} \le 0$, which requires $\lambda_{\mathrm{f}} \ge (1-2\bar{a}\bar{\omega}M)r$ and $\lambda_{\mathrm{m}} \ge (1-2\bar{a}\bar{\omega}M)r$. Therefore: it is sufficient to have $\lambda_{\mathrm{f}} > \lambda_{\mathrm{m}}$ or $\lambda_{\mathrm{f}} < \lambda_{\mathrm{m}}$ for $m_{\mathrm{f}}^* = m_{\mathrm{m}}^* = 0$.

ii) $m_{\mathrm{f}}^* = 0$ and $0 < m_{\mathrm{m}}^* < 1$; then $\theta_{\mathrm{f}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} \le 0$ and $\theta_{\mathrm{m}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} = 0$, which requires $\lambda_{\mathrm{f}} \ge (1-2\bar{a}\bar{\omega}M)r$ and $\lambda_{\mathrm{m}} < (1-2\bar{a}\bar{\omega}M)r$. Therefore: $\lambda_{\mathrm{f}} > \lambda_{\mathrm{m}}$.

iv) $0 < m_{\mathrm{f}}^* < 1$ and $m_{\mathrm{m}}^* = 0$; then $\theta_{\mathrm{f}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} = 0$ and $\theta_{\mathrm{m}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} \le 0$, which requires $\lambda_{\mathrm{f}} < (1-2\bar{a}\bar{\omega}M)r$ and $\lambda_{\mathrm{m}} \ge (1-2\bar{a}\bar{\omega}M)r$. Therefore: $\lambda_{\mathrm{f}} < \lambda_{\mathrm{m}}$.

v) $0 < m_{\mathrm{f}}^* < 1$ and $0 < m_{\mathrm{m}}^* < 1$; then $\theta_{\mathrm{f}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} = 0$ and $\theta_{\mathrm{m}}|_{m_{\mathrm{f}}=m_{\mathrm{f}}^*, m_{\mathrm{m}}=m_{\mathrm{m}}^*} = 0$, which requires $m_{\mathrm{f}}^* = 1 - \lambda_{\mathrm{f}}/(1 - 2\bar{a}\bar{\omega}M)r$ and $m_{\mathrm{m}}^* = 1 - \lambda_{\mathrm{m}}/(1 - 2\bar{a}\bar{\omega}M)r$. Therefore: $m_{\mathrm{f}}^* > m_{\mathrm{m}}^*$ if and only if $\lambda_{\mathrm{f}} < \lambda_{\mathrm{m}}$ and $m_{\mathrm{f}}^* < m_{\mathrm{m}}^*$ if and only if $\lambda_{\mathrm{f}} > \lambda_{\mathrm{m}}$.

As $\lambda_{\mathrm{f}} < \lambda_{\mathrm{m}}$ obtains in every scenario in which $m_{\mathrm{f}}^* \geq m_{\mathrm{m}}^*$, and as $\lambda_{\mathrm{f}} > \lambda_{\mathrm{m}}$ obtains in every scenario in which $m_{\mathrm{f}}^* \leq m_{\mathrm{m}}^*$, we have demonstrated that $\lambda_{\mathrm{f}} < \lambda_{\mathrm{m}}$ is a sufficient condition for $m_{\mathrm{f}}^* \geq m_{\mathrm{m}}^*$ and $\lambda_{\mathrm{f}} > \lambda_{\mathrm{m}}$ is a sufficient condition for $m_{\mathrm{f}}^* \leq m_{\mathrm{m}}^*$, when $M_{\mathrm{f}} = M_{\mathrm{m}} = M$.

We now demonstrate that it is also true that $\lambda_{\mathrm{f}} \leq \lambda_{\mathrm{m}}$ is a sufficient condition for $d_{\mathrm{f}}^* \geq d_{\mathrm{m}}^*$ and that $\lambda_{\mathrm{f}} \geq \lambda_{\mathrm{m}}$ is a sufficient condition for $d_{\mathrm{f}}^* \leq d_{\mathrm{m}}^*$, when $M_{\mathrm{f}} = M_{\mathrm{m}} = M$. the marginal fitness function for female dispersal is $\theta_{\mathrm{f}} = -\lambda_{\mathrm{f}} + (1 - d_{\mathrm{f}})(1 - 2\bar{a}\bar{\omega}M)r/(1 - d_{\mathrm{f}}\,\lambda_{\mathrm{f}})$ and the marginal fitness function for male dispersal is $\theta_{\mathrm{m}} = -\lambda_{\mathrm{m}} + (1 - d_{\mathrm{m}})(1 - 2\bar{a}\bar{\omega}M)r/(1 - d_{\mathrm{m}}\,\lambda_{\mathrm{m}})$. We consider all possible cases. Analogously to the previous demonstration, cases iii), vi), vii), viii), and ix) lead to a contradiction. We consider the remaining cases:

i) $d_{\mathrm{f}}^* = 0$ and $d_{\mathrm{m}}^* = 0$; then $\theta_{\mathrm{f}}|_{d_{\mathrm{f}}=d_{\mathrm{f}}^*, d_{\mathrm{m}}=d_{\mathrm{m}}^*} \leq 0$ and $\theta_{\mathrm{m}}|_{d_{\mathrm{f}}=d_{\mathrm{f}}^*, d_{\mathrm{m}}=d_{\mathrm{m}}^*} \leq 0$, which requires $\lambda_{\mathrm{f}} \geq (1 - 2\bar{a}\bar{\omega}M)r$ and $\lambda_{\mathrm{m}} \geq (1 - 2\bar{a}\bar{\omega}M)r$. Therefore: it is sufficient to have $\lambda_{\mathrm{f}} > \lambda_{\mathrm{m}}$, $\lambda_{\mathrm{f}} < \lambda_{\mathrm{m}}$ or $\lambda_{\mathrm{f}} = \lambda_{\mathrm{m}}$ for $d_{\mathrm{f}}^* = d_{\mathrm{m}}^* = 0$.

ii) $d_{\mathrm{f}}^* = 0$ and $0 < d_{\mathrm{m}}^* < 1$; then $\theta_{\mathrm{f}}|_{d_{\mathrm{f}}=d_{\mathrm{f}}^*, d_{\mathrm{m}}=d_{\mathrm{m}}^*} \leq 0$ and $\theta_{\mathrm{m}}|_{d_{\mathrm{f}}=d_{\mathrm{f}}^*, d_{\mathrm{m}}=d_{\mathrm{m}}^*} = 0$, which requires $\lambda_{\mathrm{f}} \geq (1 - 2\bar{a}\bar{\omega}M)r$ and $(1 - 2\bar{a}\bar{\omega}M)r = \lambda_{\mathrm{m}}(1 - d_{\mathrm{m}}^*\,\lambda_{\mathrm{m}})/(1 - d_{\mathrm{m}}^*)$. Since $(1 - d_{\mathrm{m}}^*\,\lambda_{\mathrm{m}})/(1 - d_{\mathrm{m}}^*) \geq 1$, this implies $(1 - 2\bar{a}\bar{\omega}M)r \geq \lambda_{\mathrm{m}}$. Therefore: $\lambda_{\mathrm{f}} \geq \lambda_{\mathrm{m}}$.

iv) $0 < d_{\mathrm{f}}^* < 1$ and $d_{\mathrm{m}}^* = 0$; then $\theta_{\mathrm{f}}|_{d_{\mathrm{f}}=d_{\mathrm{f}}^*, d_{\mathrm{m}}=d_{\mathrm{m}}^*} = 0$ and $\theta_{\mathrm{m}}|_{d_{\mathrm{f}}=d_{\mathrm{f}}^*, d_{\mathrm{m}}=d_{\mathrm{m}}^*} \leq 0$, which requires $(1 - 2\bar{a}\bar{\omega}M)r = \lambda_{\mathrm{f}}(1 - d_{\mathrm{f}}^*\,\lambda_{\mathrm{f}})/(1 - d_{\mathrm{f}}^*)$ and $\lambda_{\mathrm{m}} \geq (1 - 2\bar{a}\bar{\omega}M)r$. Since $(1 - d_{\mathrm{f}}^*\,\lambda_{\mathrm{f}})/(1 - d_{\mathrm{f}}^*) \geq 1$, this implies $(1 - 2\bar{a}\bar{\omega}M)r \geq \lambda_{\mathrm{f}}$. Therefore: $\lambda_{\mathrm{f}} \leq \lambda_{\mathrm{m}}$.

v) $0 < d_{\mathrm{f}}^* < 1$ and $0 < d_{\mathrm{m}}^* < 1$; then $\theta_{\mathrm{f}}|_{d_{\mathrm{f}}=d_{\mathrm{f}}^*, d_{\mathrm{m}}=d_{\mathrm{m}}^*} = 0$ and $\theta_{\mathrm{m}}|_{d_{\mathrm{f}}=d_{\mathrm{f}}^*, d_{\mathrm{m}}=d_{\mathrm{m}}^*} = 0$, which requires $d_{\mathrm{f}}^* = ((1 - 2\bar{a}\bar{\omega}M)r - \lambda_{\mathrm{f}})/((1 - 2\bar{a}\bar{\omega}M)r - \lambda_{\mathrm{f}}^2)$ and $d_{\mathrm{m}}^* = ((1 - 2\bar{a}\bar{\omega}M)r -$

$\lambda_\mathrm{m})/((1-2\bar{a}\bar{\omega}M)r-\lambda_\mathrm{m}^2)$. In addition, $\theta_\mathrm{f}|_{d_\mathrm{f}=d_\mathrm{f}^*,d_\mathrm{m}=d_\mathrm{m}^*}=0$ also requires $(1-2\bar{a}\bar{\omega}M)r(1-m_\mathrm{f}^*)=\lambda_\mathrm{f}\Rightarrow (1-2\bar{a}\bar{\omega}M)r>\lambda_\mathrm{f}\Rightarrow (1-2\bar{a}\bar{\omega}M)r>\lambda_\mathrm{f}^2$. By symmetry: $(1-2\bar{a}\bar{\omega}M)r(1-m_\mathrm{m}^*)=\lambda_\mathrm{m}\Rightarrow (1-2\bar{a}\bar{\omega}M)r>\lambda_\mathrm{m}\Rightarrow (1-2\bar{a}\bar{\omega}M)r>\lambda_\mathrm{m}^2$. As a consequence: $((1-2\bar{a}\bar{\omega}M)r-\lambda)/((1-2\bar{a}\bar{\omega}M)r-\lambda^2)$ is a monotonically decreasing function of λ for all $0\leq\lambda<(1-2\bar{a}\bar{\omega}M)r\leq 1$. Therefore: $d_\mathrm{f}^* > d_\mathrm{m}^*$ if and only if $\lambda_\mathrm{f} < \lambda_\mathrm{m}$, and $d_\mathrm{f}^* < d_\mathrm{m}^*$ if and only if $\lambda_\mathrm{f} > \lambda_\mathrm{m}$.

CONVERGENCE STABILITY OF MIGRATION RATES

Here we demonstrate that it is always possible to find a pair of values of female and male costs of dispersal (λ_f, λ_m) such that any given pair of female and male migration rates (m_f, m_m) are convergence stable (Taylor, 1996; Davies and Gardner, 2016) for any given values of $\bar{a}$, $\bar{\omega}$, M_f, M_m, r. The marginal fitness function for female dispersal is $\theta_\mathrm{f}=-\lambda_\mathrm{f}+(1-2\bar{a}\bar{\omega}M_\mathrm{f})(1-m_\mathrm{f})\,r$ and the marginal fitness function for male dispersal is $\theta_\mathrm{m}=-\lambda_\mathrm{m}+(1-2\bar{a}\bar{\omega}M_\mathrm{m})(1-m_\mathrm{m})\,r$. Each migration term can assume either boundary (0 and 1) or intermediate values. Therefore, nine cases are possible. We consider them in turn:

i) $m_\mathrm{f}^* = 0$ and $m_\mathrm{m}^* = 0$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*,m_\mathrm{m}=m_\mathrm{m}^*}\leq 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*,m_\mathrm{m}=m_\mathrm{m}^*}\leq 0$, which requires $\lambda_\mathrm{f} \geq (1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r$ and $\lambda_\mathrm{m} \geq (1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r$. Since $0 \leq M_\mathrm{f}, M_\mathrm{m} \leq 0.25$, it follows that $0 \leq (1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r, (1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r \leq 1$. Therefore, we can always achieve $m_\mathrm{f}^* = 0$ and $m_\mathrm{m}^* = 0$ by setting $\lambda_\mathrm{f} = 1$ and $\lambda_\mathrm{m} = 1$.

ii) $m_\mathrm{f}^* = 0$ and $0 < m_\mathrm{m}^* < 1$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*,m_\mathrm{m}=m_\mathrm{m}^*}\leq 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*,m_\mathrm{m}=m_\mathrm{m}^*}=0$, which requires $\lambda_\mathrm{f} \geq (1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r$ and $\lambda_\mathrm{m} = (1 - m_\mathrm{m}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r$. Since $0 \leq (1 - m_\mathrm{m}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r \leq 1$, we can achieve $m_\mathrm{f}^* = 0$ and $0 < m_\mathrm{m}^* < 1$ by setting $\lambda_\mathrm{f} = 1$ and $\lambda_\mathrm{m} = (1 - m_\mathrm{m}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r$.

iii) $m_\mathrm{f}^* = 0$ and $m_\mathrm{m}^* = 1$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*,m_\mathrm{m}=m_\mathrm{m}^*}\leq 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*,m_\mathrm{m}=m_\mathrm{m}^*}\geq 0$, which requires $\lambda_\mathrm{f} \geq (1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r$ and $\lambda_\mathrm{m} = 0$. Therefore, we can achieve $m_\mathrm{f}^* = 0$ and $m_\mathrm{m}^* = 1$ by setting $\lambda_\mathrm{f} = 1$ and $\lambda_\mathrm{m} = 0$.

iv) $0 < m_\mathrm{f}^* < 1$ and $m_\mathrm{m}^* = 0$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} = 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} \leq 0$, which requires $\lambda_\mathrm{f} = (1 - m_\mathrm{f}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r$ and $\lambda_\mathrm{m} \geq (1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r$. Since $0 \leq (1 - m_\mathrm{f}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r \leq 1$, we can achieve $0 < m_\mathrm{f}^* < 1$ and $m_\mathrm{m}^* = 0$ by setting $\lambda_\mathrm{f} = (1 - m_\mathrm{f}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r$ and $\lambda_\mathrm{m} = 1$.

v) $0 < m_\mathrm{f}^* < 1$ and $0 < m_\mathrm{m}^* < 1$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} = 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} = 0$, which requires $\lambda_\mathrm{f} = (1 - m_\mathrm{f}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r$ and $\lambda_\mathrm{m} = (1 - m_\mathrm{m}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r$.

vi) $0 < m_\mathrm{f}^* < 1$ and $m_\mathrm{m}^* = 1$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} = 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} \geq 0$, which requires $\lambda_\mathrm{f} = (1 - m_\mathrm{f}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{f})r$ and $\lambda_\mathrm{m} = 0$.

vii) $m_\mathrm{f}^* = 1$ and $m_\mathrm{m}^* = 0$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} \geq 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} \leq 0$, which requires $\lambda_\mathrm{f} = 0$ and $\lambda_\mathrm{m} \geq (1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r$.

viii) $m_\mathrm{f}^* = 1$ and $0 < m_\mathrm{m}^* < 1$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} \geq 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} = 0$, which requires $\lambda_\mathrm{f} = 0$ and $\lambda_\mathrm{m} = (1 - m_\mathrm{m}^*)(1 - 2\bar{a}\bar{\omega}M_\mathrm{m})r$.

ix) $m_\mathrm{f}^* = 1$ and $m_\mathrm{m}^* = 1$; then $\theta_\mathrm{f}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} \geq 0$ and $\theta_\mathrm{m}|_{m_\mathrm{f}=m_\mathrm{f}^*, m_\mathrm{m}=m_\mathrm{m}^*} \geq 0$, which requires $\lambda_\mathrm{f} = 0$ and $\lambda_\mathrm{m} = 0$.

Therefore, in every case, there exist values in the range $0 \leq \lambda_\mathrm{f}, \lambda_\mathrm{m} \leq 1$ that satisfy these requirements, and hence any desired m_f^* and m_m^* may be obtained, irrespective of the values of $\bar{a}$, $\bar{\omega}$, M_f, M_m, r, by choosing appropriate values of λ_f and λ_m.

INDIVIDUAL-BASED SIMULATIONS FOR DISPERSAL EVOLUTION

We develop an individual-based simulation model of dispersal evolution for the purpose of illustration and to assess the robustness of our analytical results. We consider a population of $p = 400$ groups, each containing $N_\mathrm{f} = 10$ adult females and $N_\mathrm{m} = 10$ adult males. Each individual carries two loci, one controlling female dispersal and the other controlling male dispersal; each locus has two alleles, each of which is represented by a real-valued number, multiple of 0.02, lying between 0 and 1, including the extremes. At initialisation, all allele values are assigned a randomly-chosen allowed value. Each adult female produces $k = 100$ daughters and $k = 100$ sons, mating randomly each time, so that the offspring of the same mother do not always share the same father (absolute promiscuity). When each offspring is produced, each gene mutates with probability $M = 0.001$ to a new value, which can be the current value, the current value + 0.02, or the current value – 0.02, with equal probability. Subadult females disperse from the natal group with a probability determined by the average of her female dispersal alleles and reach a randomly-selected group with probability $1 - \lambda_f$; subadult males disperse from the natal group with a probability determined by the average of his male dispersal alleles and reach a randomly-selected group with probability $1 - \lambda_m$. Warfare is modelled as follows: for tractability, we imagine that all groups are arranged in a circle (at every generation the order of groups is randomised, to avoid neighbour effects); each group attacks the next one in the circle clockwise and wins the war with probability $\omega = 0.5$; each individual is assigned a competitiveness value in their own group (“home”), which depends on whether the group has been attacked and which group won, and a competitiveness value in the neighbouring group (“abroad”), which depends on whether the focal group has attacked that group and which group won (see Methods). During the following phase (density dependent regulation), $N_f = 10$ females are randomly sampled (using competitiveness values as weights) to become adults; analogously $N_m = 10$ males are randomly sampled (using competitiveness values as weights) to become adults. These then produce the next generation of subadults in the following cycle. We track $G = 10{,}000$ generations of evolution and calculate average allelic values of both male and female dispersal genes in each generation. The data points shown in Figure A2.2 come from a single simulation and are the mean of the average allelic values of the last 1000 generations of evolution. The simulation code (*Wolfram Mathematica* file) is available online at: http://rspb.royalsocietypublishing.org/content/284/1849/20162699.figures-only.

Simulation results show a reasonable fit with our analytical predictions (Fig. A2.2) and the evolutionary trajectories followed are the ones expected from vector field plots

(Fig. A2.3-A2.4). The small discrepancies between the simulation data and corresponding analytical predictions owe to random drift and spontaneous mutation, neither of which are considered in our mathematical analysis.

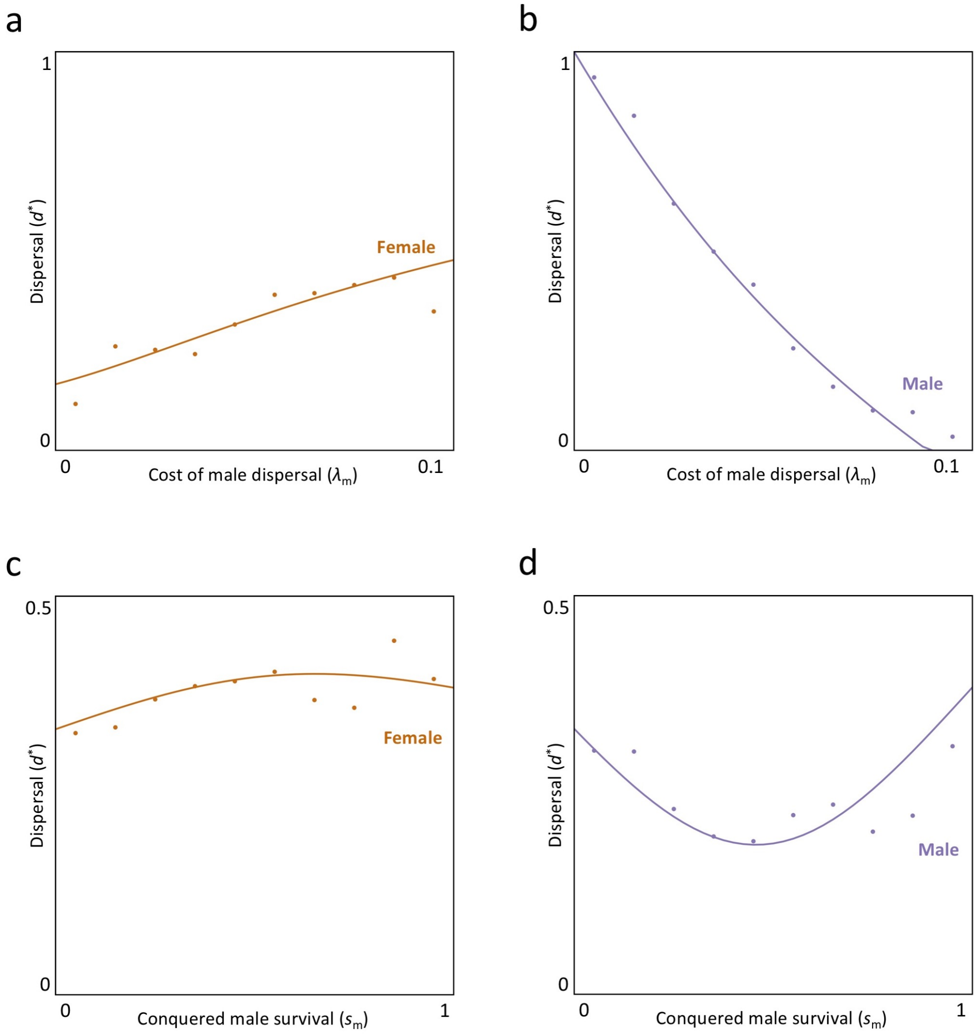

Figure A2.2 – Evolution of sex-biased dispersal and migration. Analytical predictions (lines) and individual-based simulation results (filled circles) for convergence-stable levels of female dispersal (d_f^*, orange) and male dispersal (d_m^*, purple) as a function of cost of male dispersal (λ_m; panels a-b; other parameter values are $\lambda_f = 0.05$, $s_f = 1$, $s_m = 0$, $N_f = N_m = 10$, $\bar{a} = 1$, $\bar{\omega} = 0.5$) and the probability that a conquered male obtains a breeding spot (s_m; panels c-d; other parameter values are $\lambda_f = \lambda_m = 0.05$, $s_f = 1$, $N_f = N_m = 10$, $\bar{a} = 1$, $\bar{\omega} = 0.5$).

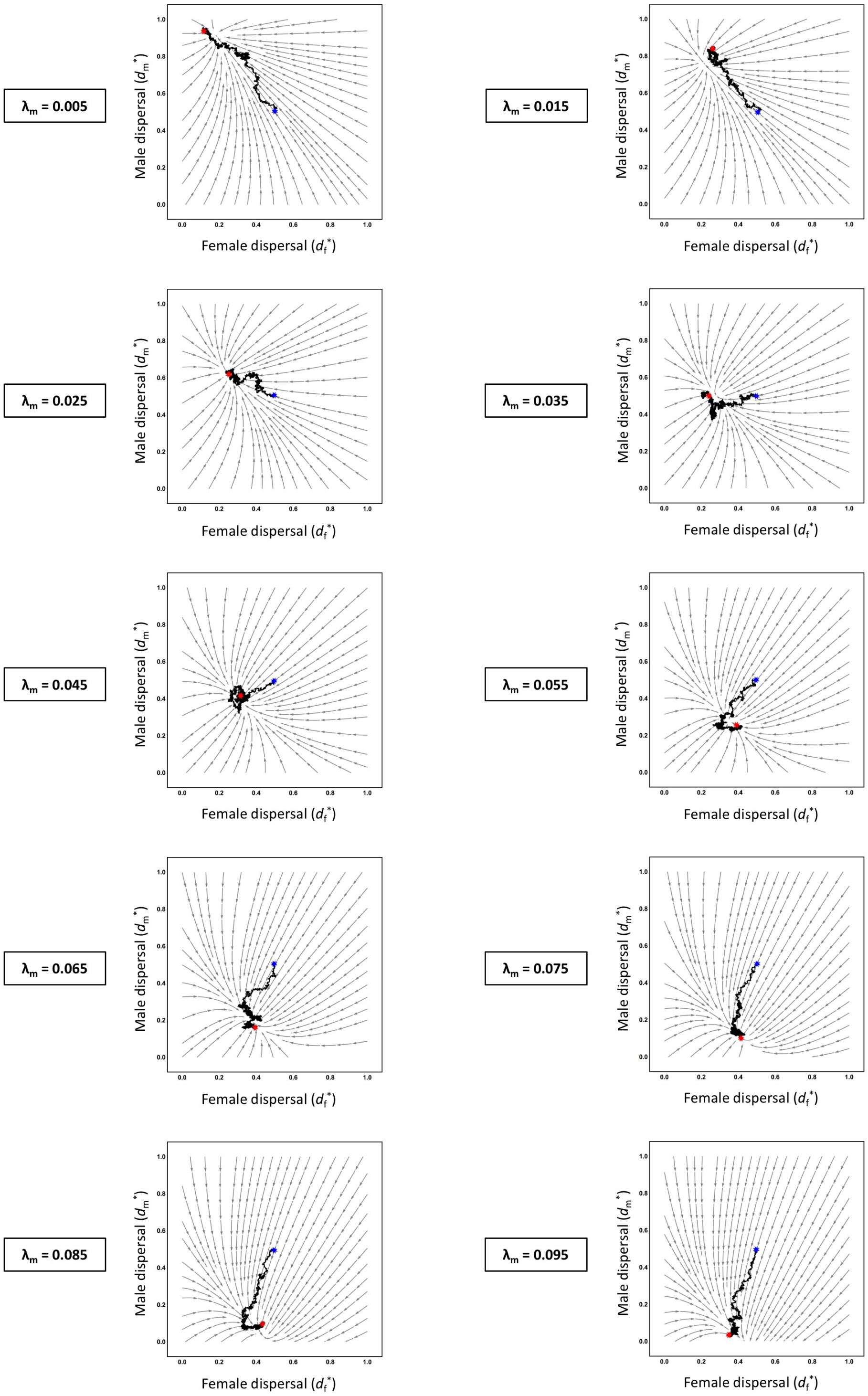

Figure A2.3 – Dispersal evolution with varying male costs of dispersal. Vector field plots and evolutionary trajectories of female dispersal (d_f^*) and male dispersal (d_m^*) resulting from individual-based simulations, for different values of male cost of dispersal λ_m. Blue star indicates average allelic values at the start of the simulation; black dots indicate average allelic value in each successive generation; red star indicates average allelic values in the last generation. Parameter values: λ_f = 0.05, s_f = 1, s_m = 0, N_f = N_m = 10, $\bar{a}$ = 1, $\bar{\omega}$ = 0.5.

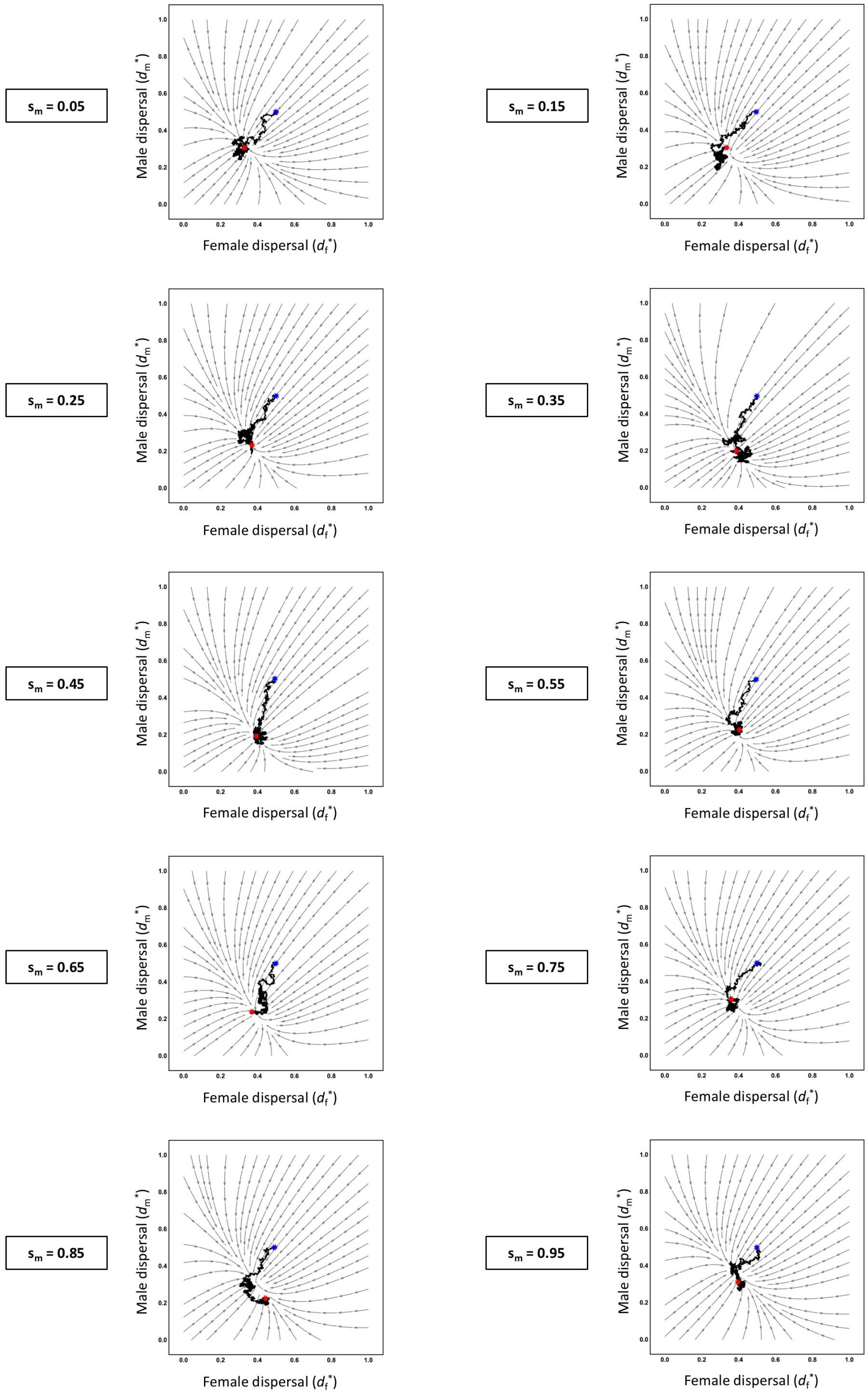

Figure A4.3.3 – Dispersal evolution with varying conquered male survival. Vector field plots and evolutionary trajectories of female dispersal (d_f^*) and male dispersal (d_m^*) resulting from individual-based simulations, for different values of conquered male survival s_m. Blue star indicates average allelic values at the start of the simulation; black dots indicate average allelic value in each successive generation; red star indicates average allelic values in the last generation. Parameter values: $\lambda_f = \lambda_m = 0.05$, $s_f = 1$, $N_f = N_m = 10$, $\bar{a} = 1$, $\bar{\omega} = 0.5$.

Belligerence

MARGINAL FITNESS

Now, consider that the locus $\mathcal{G}$ controls belligerence (the phenotype is exhibited only by males). Assuming vanishing genetic variation, the direction of natural selection is given by equation [A2.3] with all derivatives evaluated at $g = g_{\mathrm{m}} = g_{\mathrm{f}} = \bar{G}$.

The derivative $\mathrm{d}W_{\mathrm{f}}/\mathrm{d}g_{\mathrm{f}}$ (in equation [A2.3]) describes how the genic value of a gene drawn from a subadult female impacts on her relative fitness. Since females carry the gene, but do not express it, only indirect fitness is considered. This depends on the association between the belligerence phenotype of a male randomly sampled from the focal group and the focal female's relative fitness, the association between the breeding value of that male's controller and that male's belligerence phenotype, and the association between the breeding value of that male's controller and the focal female's genic value. This can be expressed mathematically:

$$\frac{\mathrm{d}W_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} = \frac{\partial W_{\mathrm{f}}}{\partial A'}\frac{\mathrm{d}A'}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_{\mathrm{f}}} = \frac{\partial W_{\mathrm{f}}}{\partial A'}\, p_{\mathrm{female|controller}}\, \gamma\,, \qquad \text{[A2.13]}$$

where $p_{\mathrm{female|controller}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{f}}$ is the consanguinity between the focal female and the controller of a random male in her group, and $\gamma = \mathrm{d}A'/\mathrm{d}G'$ is again the association between an individual's phenotype and its controller's breeding value.

The derivative $\mathrm{d}W_{\mathrm{m}}/\mathrm{d}g_{\mathrm{m}}$ (in equation [A2.3]) describes how the genic value of a gene drawn from a subadult male impacts on his relative fitness. It depends on i) the association between the belligerence phenotype of the focal male and his own relative fitness, the association between the breeding value for the belligerence gene of the male's controller and the focal male's belligerence phenotype, the association between the genic value of the focal male and the breeding value of his controller, and ii) the association between the belligerence phenotype of a random male in the focal group and the focal male's relative fitness, the association between the breeding value for the belligerence gene of the random male's controller and the random male's belligerence phenotype, the association between the genic value of the focal male and the breeding value of the random male's controller. This can be expressed mathematically:

$$\frac{\mathrm{d}W_\text{m}}{\mathrm{d}g_\text{m}} = \frac{\partial W_\text{m}}{\partial A}\frac{\mathrm{d}A}{\mathrm{d}G}\frac{\mathrm{d}G}{\mathrm{d}g_\text{m}} + \frac{\partial W_\text{m}}{\partial A'}\frac{\mathrm{d}A'}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_\text{m}} = \left(\frac{\partial W_\text{m}}{\partial A} p_\text{focal|controller} + \frac{\partial W_\text{m}}{\partial A'} p_\text{male|controller}\right)\gamma\,, \quad \text{[A2.14]}$$

where $p_\text{focal|controller} = \mathrm{d}G/\mathrm{d}g_\text{m}$ is the consanguinity between the focal male and his controller, $p_\text{male|controller} = \mathrm{d}G'/\mathrm{d}g_\text{m}$ is the consanguinity between the focal male and the controller of a random male in his group, and $\gamma = \mathrm{d}A'/\mathrm{d}G'$ is the correlation between an individual's phenotype and its controller's breeding value.

Considering that both a and t are functions of A, it results that $\partial W_\text{f}/\partial A' = (\partial W_\text{f}/\partial a')(\partial a'/\partial A')$, $\partial W_\text{m}/\partial A = (\partial W_\text{m}/\partial t(A))(\partial t(A)/\partial A)$, and $\partial W_\text{m}/\partial A' = (\partial W_\text{m}/\partial a')(\partial a'/\partial A') + (\partial W_\text{m}/\partial t(A'))(\partial t(A')/\partial A')$, where $\partial t(A)/\partial A = \partial t(A')/\partial A' = -\,t(\bar{A})\,c_\text{a}$ and $\partial a'/\partial A' = b_\text{a}$. Substituting these expressions and equations [A2.12-A2.13] into equation [A2.3], we obtain:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_\text{f}\frac{\partial W_\text{f}}{\partial a'} b_\text{a}\, p_\text{female|controller}\,\gamma + c_\text{m}\left(\frac{\partial W_\text{m}}{\partial t(A)}\left(-t(\bar{A})\,c_\text{a}\right) p_\text{focal|controller} + \left(\frac{\partial W_\text{m}}{\partial a'} b_\text{a} + \frac{\partial W_\text{m}}{\partial t(A')}\left(-t(\bar{A})\,c_\text{a}\right)\right) p_\text{male|controller}\right)\gamma\,. \quad \text{[A2.15]}$$

The condition for an increase in population average female dispersal is $\mathrm{d}W/\mathrm{d}g > 0$ and, as $c_\text{f} = c_\text{m} = 1/2$ under diploid inheritance, this condition is equivalent to:

$$-c_\text{a}\, p_\text{focal|controller} + \left(1 - 2\,\bar{a}\,\bar{\omega}\,s_\text{m}\,(1 - s_\text{m})\right) c_\text{a}\, p_\text{male|controller} + \bar{\omega}\,(1 - s_\text{m})\, b_\text{a}\, p_\text{male|controller} + \bar{\omega}\,(1 - s_\text{f})\, b_\text{a} p_\text{female|controller} > 0\,. \quad \text{[A2.16]}$$

Dividing by $p_\text{focal|controller}$ to obtain $R_\text{male|controller} = p_\text{male|controller}/p_\text{focal|controller}$ and $R_\text{female|controller} = p_\text{femal|controller}/p_\text{focal|controller}$ (see CONSANGUINITY AND RELATEDNESS) yields condition [2.3] in Results.

Condition [A2.16] can be rearranged as follows:

$$\frac{c_\mathrm{a}}{b_\mathrm{a}} < \frac{\bar{\omega}(1-m_\mathrm{m})^2\big((1-s_\mathrm{m})\, p_\mathrm{male|controller}+(1-s_\mathrm{f})\, p_\mathrm{female|controller}\big)}{(1-m_\mathrm{m})^2\, p_\mathrm{focal|controller}-\varphi_\mathrm{MM}\, p_\mathrm{male|controller}}, \qquad \text{[A2.17]}$$

where $\varphi_\mathrm{MM} = (1 - 2\, \bar{a}\, \bar{\omega}\, s_\mathrm{m}\, (1 - s_\mathrm{m}))(1 - m)^2$ is the probability that two males in a post-competition group were born in the same group. The right-hand side of [A2.17] can be conceptualised as "potential for belligerence" (cf. Gardner, 2010) and is termed λ_A.

Substituting $p_\mathrm{focal|controller}$, $p_\mathrm{female|controller}$, and $p_\mathrm{male|controller}$ in [A2.17] with the appropriate consanguinities (see CONSANGUINITY AND RELATEDNESS) yields the condition for increase of the belligerence gene. When the phenotype is controlled by the genotype of the father of the focal individual (p_s, $p_\mathrm{female|faher}$, $p_\mathrm{male|father}$) this is:

$$\frac{c_\mathrm{a}}{b_\mathrm{a}} < \frac{\bar{\omega}(1-m_\mathrm{m})\big((1-s_\mathrm{m})(1-m_\mathrm{m})+(1-s_\mathrm{f})(1-m_\mathrm{f})\big)(4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)-2N_\mathrm{m}N_\mathrm{f}\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})(\varphi_\mathrm{MF}+\varphi_\mathrm{MM})(N_\mathrm{m}-1)}{(N_\mathrm{m}-\varphi_\mathrm{MM})(4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}-2N_\mathrm{m}N_\mathrm{f}\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})\varphi_\mathrm{MF})-\varphi_\mathrm{MM}(N_\mathrm{m}+N_\mathrm{f})(\varphi_\mathrm{MF}+\varphi_\mathrm{MM})(N_\mathrm{m}-1)}. \qquad \text{[A2.18]}$$

Setting $m_\mathrm{f} = m_\mathrm{m} = m$ and assuming that $N_\mathrm{f} = N_\mathrm{m} = N$ is large, thus neglecting terms of order $1/N^2$, these reduce to:

$$\frac{c_\mathrm{a}}{b_\mathrm{a}} < \frac{2\bar{\omega}x(1-m)^2\Big(1+\frac{1}{2}\bar{a}\,\bar{\omega}(1-m)^2(s_\mathrm{f}-s_\mathrm{m})(1-s_\mathrm{f}-s_\mathrm{m})\Big)}{N\Big(1-(1-m)^2\big(1-2\bar{a}\bar{\omega}x(1-x)\big)\Big)}, \qquad \text{[A2.19]}$$

where $x = 1 - (s_\mathrm{m} + s_\mathrm{f})/2$. Noting that $b_\mathrm{a} = \bar{a}\, B_\mathrm{a} / (1 - m_\mathrm{m})$ and $c_\mathrm{a} = C_\mathrm{a}$ in Lehmann & Feldman's (2008) notation, this recovers their result see (see equation (2.2) in Lehmann and Feldman (2009)).

When the phenotype is controlled by the genotype of the mother of the focal individual (p_s, $p_\mathrm{female|mother}$, $p_\mathrm{male|mother}$) the condition is given by:

$$\frac{c_\mathrm{a}}{b_\mathrm{a}} < \frac{\bar{\omega}(1-m_\mathrm{m})\big((1-s_\mathrm{m})(1-m_\mathrm{m})+(1-s_\mathrm{f})(1-m_\mathrm{f})\big)(4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)-2N_\mathrm{m}N_\mathrm{f}\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})(\varphi_\mathrm{MF}+\varphi_\mathrm{FF})(N_\mathrm{f}-1)}{(N_\mathrm{f}-\varphi_\mathrm{MM})(4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}-2N_\mathrm{m}N_\mathrm{f}\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})\varphi_\mathrm{MF})-\varphi_\mathrm{MM}(N_\mathrm{m}+N_\mathrm{f})(\varphi_\mathrm{MF}+\varphi_\mathrm{FF})(N_\mathrm{f}-1)}. \qquad \text{[A2.20]}$$

When the genotype of the focal individual controls the phenotype (p_I, $p_\mathrm{female|individual}$, $p_\mathrm{male|individual}$) this is:

$$\frac{c_{\mathrm{a}}}{b_{\mathrm{a}}} < \frac{2\bar{\omega}(1-m_{\mathrm{m}})\big((1-s_{\mathrm{m}})(1-m_{\mathrm{m}})+(1-s_{\mathrm{f}})(1-m_{\mathrm{f}})\big)(N_{\mathrm{f}}+N_{\mathrm{m}})}{4N_{\mathrm{m}}N_{\mathrm{f}}-N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}-2N_{\mathrm{m}}N_{\mathrm{f}}\varphi_{\mathrm{MF}}+(N_{\mathrm{m}}+N_{\mathrm{f}})\varphi_{\mathrm{MF}}}\ . \qquad [A2.21]$$

Finally, granting full control over the phenotype to paternal-origin genes ($p_{\mathrm{I|paternal}}$, $p_{\mathrm{female|paternal}}$, $p_{\mathrm{male|paternal}}$) we have:

$$\frac{c_{\mathrm{a}}}{b_{\mathrm{a}}} < \frac{\bar{\omega}(1-m_{\mathrm{m}})\big((1-s_{\mathrm{m}})(1-m_{\mathrm{m}})+(1-s_{\mathrm{f}})(1-m_{\mathrm{f}})\big)(4N_{\mathrm{m}}N_{\mathrm{f}}-N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}+(N_{\mathrm{f}}+N_{\mathrm{m}})(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}+N_{\mathrm{m}}(N_{\mathrm{m}}-N_{\mathrm{f}})\varphi_{\mathrm{MF}})}{N_{\mathrm{m}}(8N_{\mathrm{f}}N_{\mathrm{m}}-2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}-4N_{\mathrm{f}}N_{\mathrm{m}}\varphi_{\mathrm{MF}})-\varphi_{\mathrm{MM}}(4N_{\mathrm{f}}N_{\mathrm{m}}-N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}+(N_{\mathrm{f}}+N_{\mathrm{m}})(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}+N_{\mathrm{m}}(N_{\mathrm{m}}-N_{\mathrm{f}})\varphi_{\mathrm{MF}})}\ . \qquad [A2.22]$$

and granting full control over the phenotype to paternal-origin genes ($p_{\mathrm{I|maternal}}$, $p_{\mathrm{female|maternal}}$, $p_{\mathrm{male|maternal}}$), we obtain:

$$\frac{c_{\mathrm{a}}}{b_{\mathrm{a}}} < \frac{\bar{\omega}(1-m_{\mathrm{m}})\big((1-s_{\mathrm{m}})(1-m_{\mathrm{m}})+(1-s_{\mathrm{f}})(1-m_{\mathrm{f}})\big)(4N_{\mathrm{m}}N_{\mathrm{f}}-N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}+(N_{\mathrm{f}}+N_{\mathrm{m}})(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}+N_{\mathrm{f}}(N_{\mathrm{f}}-N_{\mathrm{m}})\varphi_{\mathrm{MF}})}{N_{\mathrm{f}}(8N_{\mathrm{f}}N_{\mathrm{m}}-2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}-4N_{\mathrm{f}}N_{\mathrm{m}}\varphi_{\mathrm{MF}})-\varphi_{\mathrm{MM}}(4N_{\mathrm{f}}N_{\mathrm{m}}-N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}+(N_{\mathrm{f}}+N_{\mathrm{m}})(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}+N_{\mathrm{f}}(N_{\mathrm{f}}-N_{\mathrm{m}})\varphi_{\mathrm{MF}})}\ . \qquad [A2.23]$$

CONSANGUINITY AND RELATEDNESS

The consanguinity of a focal subadult, independent of sex, to a parent is given by $p_{\mathrm{S}} = \frac{1}{2}(\frac{1}{2}(1+f)) + \frac{1}{2}f$ (where f is the inbreeding coefficient). The consanguinity of the focal subadult male to a random subadult male in his post-migration group is equal to the probability that they were born in the same group and that neither migrated, namely $p_{\mathrm{male|individual}} = (1-m_{\mathrm{m}})^2\, p_{\mathrm{X}}$. The consanguinity of the focal subadult male to a random subadult male in his post-migration group is derived analogously and is given by $p_{\mathrm{female|individual}} = (1-m_{\mathrm{f}})^2\, p_{\mathrm{X}}$. Substituting [A2.7] in $p_{\mathrm{male|individual}}$ and $p_{\mathrm{female|individual}}$, we obtain explicit expressions (Table A2.1). Dividing $p_{\mathrm{male|individual}}$ and $p_{\mathrm{female|individual}}$ by p_{I} yields relatedness coefficients $R_{\mathrm{male|individual}}$ and $R_{\mathrm{female|individual}}$ in their explicit form (Table A2.1).

The consanguinity of a focal subadult male to the father of a random subadult male in their post-migration group is given by:

$$p_{\mathrm{male|father}} = (1-m_{\mathrm{m}})^2\left(\frac{1}{N_{\mathrm{m}}}p_{\mathrm{S}} + \frac{(N_{\mathrm{m}}-1)(f+p_{\mathrm{MM}})}{2N_{\mathrm{m}}}\right). \qquad [A2.24]$$

That is, with probability $(1-m_\mathrm{m})^2$ both the focal male and his male groupmate were born in the same group: in this case, with probability $1/N_\mathrm{m}$ they share the same father and hence the consanguinity between the focal subadult male and his father is p_S; alternatively, with probability $(N_\mathrm{m}-1)/N_\mathrm{m}$ the two males do not have the same father and hence the consanguinity of the focal subadult male with the father of the other male is equal to $(f+p_\mathrm{MM})/2$. A similar rationale is followed to obtain the consanguinity of a focal subadult female to the father of a random subadult male in their group:

$$p_\text{female|father} = (1-m_\mathrm{m})(1-m_\mathrm{f})\left(\frac{1}{N_i}p_\mathrm{S} + \frac{(N_\mathrm{m}-1)(f+p_\mathrm{MM})}{2N_\mathrm{m}}\right). \qquad \text{[A2.25]}$$

The consanguinities of a subadult male and a subadult female to the mother of a random subadult male in the group are derived analogously:

$$p_\text{male|mother} = (1-m_\mathrm{m})^2\left(\frac{1}{N_\mathrm{f}}p_\mathrm{S} + \frac{(N_\mathrm{f}-1)(f+p_\mathrm{FF})}{2N_\mathrm{f}}\right), \qquad \text{[A2.26]}$$

$$p_\text{female|mother} = (1-m_\mathrm{m})(1-m_\mathrm{f})\left(\frac{1}{N_\mathrm{f}}p_\mathrm{S} + \frac{(N_\mathrm{f}-1)(f+p_\mathrm{FF})}{2N_\mathrm{f}}\right). \qquad \text{[A2.27]}$$

Substituting the appropriate consanguinities, including [A2.7], in the equations above yields p_s, $p_\text{male|father}$, $p_\text{female|father}$, $p_\text{male|mother}$, and $p_\text{female|mother}$ in their explicit form (Table A2.2). Dividing $p_\text{male|father}$, $p_\text{female|father}$, $p_\text{male|mother}$, and $p_\text{female|mother}$ by p_s, yields $R_\text{male|father}$, $R_\text{female|father}$, $R_\text{male|mother}$, and $R_\text{female|mother}$, respectively, in their explicit form (Table A2.2).

The consanguinities of a focal individual to its paternal-origin genes $p_\text{I|paternal}$ and to its maternal-origin genes $p_\text{I|maternal}$ are both equal to p_I, the consanguinity of a focal individual to herself (Table A2.3). The consanguinity between a focal subadult male and the paternal-origin genes of a random subadult male in his group $p_\text{male|paternal}$ is given by

$$p_\text{male|paternal} = (1-m_\mathrm{m})^2\left(\frac{1}{2}\left(\frac{1}{N_\mathrm{m}}p_\mathrm{I} + \frac{N_\mathrm{m}-1}{N_\mathrm{m}}p_\mathrm{MM}\right) + \frac{1}{2}f\right). \qquad \text{[A2.28]}$$

That is with probability $(1 - m_{\mathrm{m}})^2$ both the focal male and his male groupmate were born in the same group. And with probability 1/2, a gene picked from the focal male is the paternal gene: in this case, with probability $1/N_{\mathrm{m}}$, the two males share the same father and so the gene is identical-by-descent to the paternal-origin gene in the random male with probability p_{I}; alternatively, with probability $(N_{\mathrm{m}} - 1)/N_{\mathrm{m}}$, the two males do not share the same father and therefore the probability of identity-by-descent between the gene we have picked and the paternal-origin gene in the random male is p_{FF}. On the other hand, with probability 1/2, a gene picked from the focal male is the maternal gene: in this case, the gene is identical-by-descent to the paternal-origin gene of the random male with probability f. The consanguinity between a focal subadult female and the paternal-origin genes of a random subadult male in her group $p_{\mathrm{female|paternal}}$ is derived analogously:

$$p_{\mathrm{female|paternal}} = (1 - m_{\mathrm{m}})(1 - m_{\mathrm{f}}) \left(\frac{1}{2} \left(\frac{1}{N_{\mathrm{m}}} p_{\mathrm{I}} + \frac{N_{\mathrm{m}}-1}{N_{\mathrm{m}}} p_{\mathrm{MM}} \right) + \frac{1}{2} f \right) . \qquad \text{[A2.29]}$$

Finally, the same rationale is followed to derive the consanguinities of a focal individual to the maternal-origin genes of a random male in its group. These are given by:

$$p_{\mathrm{male|maternal}} = (1 - m_{\mathrm{m}})^2 \left(\frac{1}{2} \left(\frac{1}{N_{\mathrm{f}}} p_{\mathrm{I}} + \frac{N_{\mathrm{f}}-1}{N_{\mathrm{f}}} p_{\mathrm{FF}} \right) + \frac{1}{2} f \right) , \qquad \text{[A2.30]}$$

$$p_{\mathrm{male|maternal}} = (1 - m_{\mathrm{m}})(1 - m_{\mathrm{f}}) \left(\frac{1}{2} \left(\frac{1}{N_{\mathrm{f}}} p_{\mathrm{I}} + \frac{N_{\mathrm{f}}-1}{N_{\mathrm{f}}} p_{\mathrm{FF}} \right) + \frac{1}{2} f \right) . \qquad \text{[A2.31]}$$

Notice that $p_{\mathrm{female|maternal}}$ and $p_{\mathrm{female|paternal}}$ are derived in a way analogous to $p_{\mathrm{female|individual}}$, but conditional on picking the maternal-origin or paternal-origin gene, respectively, from the random female. Therefore, $p_{\mathrm{female|individual}}$ is the arithmetic mean of $p_{\mathrm{female|maternal}}$ and $p_{\mathrm{female|paternal}}$. Analogously, $p_{\mathrm{male|individual}}$ is the arithmetic mean of $p_{\mathrm{male|maternal}}$ and $p_{\mathrm{male|paternal}}$.

Substituting the appropriate consanguinities, including [A2.7], in the equations above yields $p_{\mathrm{male|paternal}}$, $p_{\mathrm{female|paternal}}$, $p_{\mathrm{male|maternal}}$, and $p_{\mathrm{female|maternal}}$ in their explicit form (Table A2.3). Dividing $p_{\mathrm{male|paternal}}$, $p_{\mathrm{female|paternal}}$, $p_{\mathrm{male|maternal}}$, and $p_{\mathrm{female|maternal}}$ by p_{I} yields $R_{\mathrm{male|paternal}}$, $R_{\mathrm{female|paternal}}$, $R_{\mathrm{male|maternal}}$, and $R_{\mathrm{female|maternal}}$, respectively, in their explicit form

(Table A2.3). Notice that $R_{\text{female|individual}}$ is the arithmetic mean of $R_{\text{female|maternal}}$ and $R_{\text{female|paternal}}$, and $R_{\text{male|individual}}$ is the arithmetic mean of $R_{\text{male|maternal}}$ and $R_{\text{male|paternal}}$.

INDIVIDUAL-BASED SIMULATIONS FOR BELLIGERENCE EVOLUTION

We develop an individual-based simulation model of belligerence evolution for the purpose of illustration and to assess the robustness of our analytical results. We consider a population of $p = 400$ groups, each containing $N_{\text{f}} = 10$ adult females and $N_{\text{m}} = 10$ adult males. Each individual carries a belligerence locus with two alleles, each of which is represented by a real-valued number, multiple of 0.02, lying between 0 and 1, including the extremes. At initialisation, all allele values are assigned a randomly-chosen allowed value. Each adult female produces $k = 100$ daughters and $k = 100$ sons, mating randomly each time, so that the offspring of the same mother do not always share the same father (absolute promiscuity). When each offspring is produced, each gene mutates with probability $M = 0.001$ to a new value, which can be the current value, the current value + 0.02, or the current value – 0.02, with equal probability. Subadult females migrate to a randomly-selected group with probability m_{f}; subadult males to a randomly-selected group probability m_{m}. Warfare is modelled as follows: for tractability, we imagine that all groups are arranged in a circle (at every generation the order of groups is randomised, to avoid neighbour effects); each group attacks the next one in the circle clockwise with a probability determined by the average belligerence allelic value of subadult males in the group; the group wins the war with probability $\omega = 0.5$; each individual is assigned a competitiveness value in their own group ("home"), which depends on whether the group has been attacked and which group won, and a competitiveness value in the neighbouring group ("abroad"), which depends on whether the focal group has attacked that group and which group won (see Methods). During the following phase (density dependent regulation), $N_{\text{f}} = 10$ females are randomly sampled (using competitiveness values as weights) to become adults; analogously $N_{\text{m}} = 10$ males are randomly sampled (using competitiveness values as weights) to become adults. These then produce the next generation of subadults in the following cycle. We track $G = 10{,}000$ generations of evolution and calculate average allelic values of belligerence in each generation. The data points shown in Figure A2.5 come from a single simulation and are the mean of the average

allelic values of the last 1000 generations of evolution. The simulation code (*Wolfram Mathematica* file) is available online at:
http://rspb.royalsocietypublishing.org/content/284/1849/20162699.figures-only.

Simulation results show a reasonable fit with our analytical predictions (Fig A2.5), given that evolutionary trajectories in the simulation model are influenced by random drift and spontaneous mutation. Simulation results are noisier under maternal and paternal control than under individual control: this conforms to our expectation that stochastic effects would be stronger under maternal and paternal control, because in these cases selection acts on a much smaller number of individuals (i.e. mothers or fathers, rather than subadults males themselves).

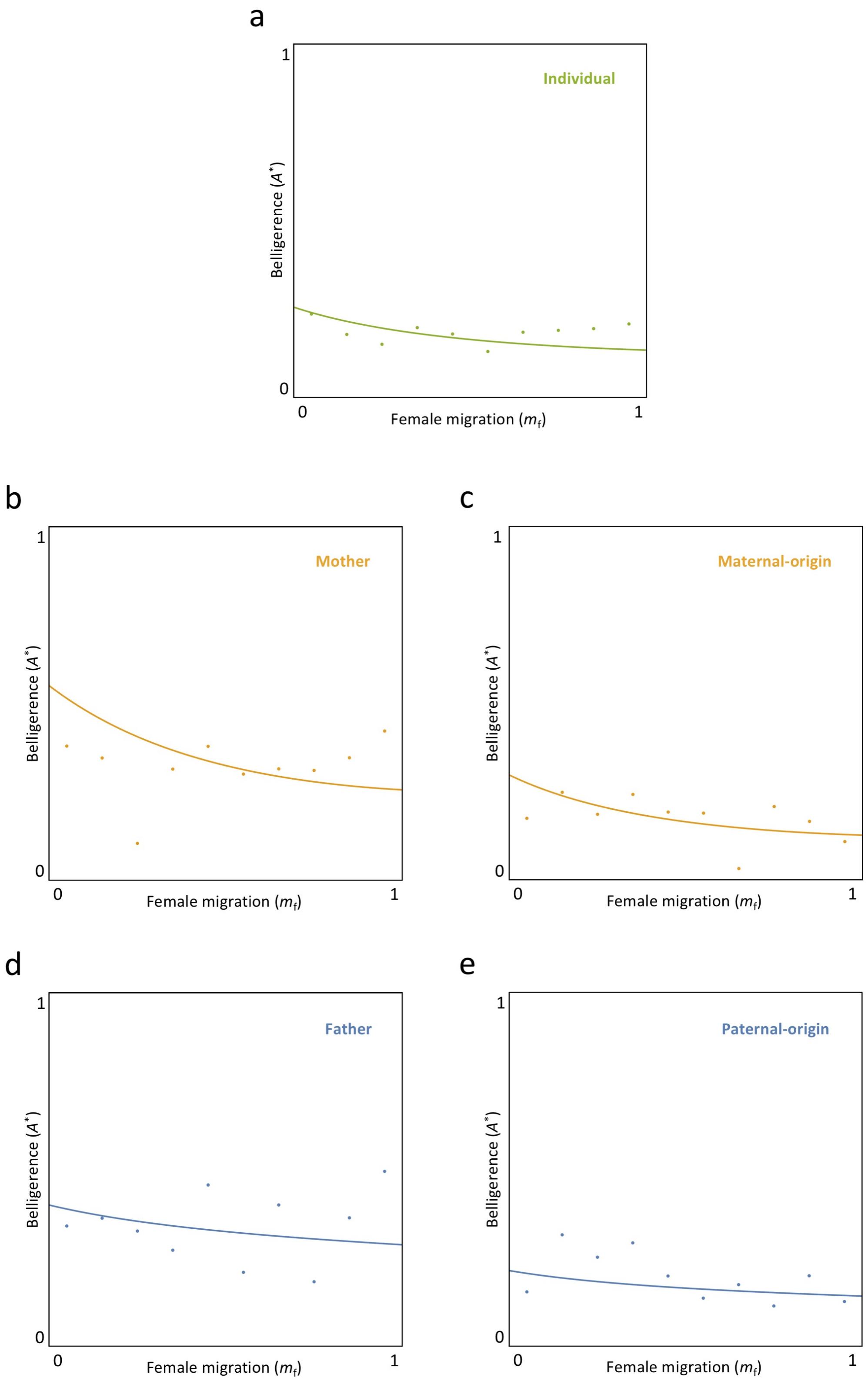

Figure A2.5 – Evolution of belligerence. Analytical predictions (lines) and individual-based simulation results (filled circles) for convergence-stable levels of belligerence (A^*) as a function of female migration (m_f) when belligerence is controlled by the focal male (panel a), his mother (panel b), his father (panel d), his maternal-origin genes (panel c), or his paternal-origin genes (panel e). Other parameter values are $\bar{\omega} = 0.5$, $m_m = 0.5$, $s_f = 1$, $s_m = 0$, $N_f = N_m = 10$. We assume functional forms $a = A_{att}$ and $t = 1 - 0.025\ a^2$.

Bravery

MARGINAL FITNESS

A procedure analogous to the one followed in section *Marginal fitness* (for belligerence) is followed to study the evolution of the bravery gene. The condition for an increase in population average bravery:

$$-c_{\omega}p_{\mathrm{focal|controller}} + \left(1 - 2\bar{\omega}s_{\mathrm{m}}(1 - s_{\mathrm{m}})\right)c_{\omega}p_{\mathrm{male|controller}} + 2(1 - s_{\mathrm{m}})b_{\omega}p_{\mathrm{male|controller}} + 2(1 - s_{\mathrm{f}})b_{\omega}p_{\mathrm{female|controller}} > 0\,, \qquad [A2.32]$$

where: $c_{\omega} = -(\partial\tau(\Omega)/\partial\Omega)/\tau(\bar{\Omega})|_{\Omega=\Omega'=\bar{\Omega}}$ and $b_{\omega} = \partial\omega(\bar{\Omega},\Omega')/\partial\Omega'|_{\Omega=\Omega'=\bar{\Omega}}$.

Condition (A32) can be rearranged as follows:

$$\frac{c_{\omega}}{b_{\omega}} < \frac{2(1-m_{\mathrm{m}})^2\left((1-s_{\mathrm{m}})\,p_{\mathrm{male|controller}}+(1-s_{\mathrm{f}})\,p_{\mathrm{female|controller}}\right)}{(1-m_{\mathrm{m}})^2\,p_{\mathrm{focal|controller}}-\tilde{\varphi}_{\mathrm{MM}}\,p_{\mathrm{male|controller}}}\,, \qquad [A2.33]$$

where $\tilde{\varphi}_{\mathrm{MM}} = (1 - 2\,\bar{\omega}\,s_{\mathrm{m}}\,(1 - s_{\mathrm{m}}))(1 - m)^2$ is the probability that two males in a post-competition group were born in the same group, conditioned on the two males being involved in a war. The right-hand side of [A2.33] can be conceptualised as the "potential for bravery" (cf. Gardner, 2010) and it is termed λ_{Ω}.

Substituting $p_{\mathrm{focal|controller}}$, $p_{\mathrm{male|controller}}$, and $p_{\mathrm{female|controller}}$ in [A2.33] with the appropriate consanguinities (see CONSANGUINITY AND RELATEDNESS above) yields the condition for increase of the bravery gene. When the phenotype is controlled by the genotype of the father of the focal individual (p_{s}, $p_{\mathrm{male|father}}$, $p_{\mathrm{female|father}}$) this is:

$$\frac{c_{\omega}}{b_{\omega}} < \frac{2(1-m_{\mathrm{m}})\left((1-s_{\mathrm{m}})(1-m_{\mathrm{m}})+(1-s_{\mathrm{f}})(1-m_{\mathrm{f}})\right)\left(4N_{\mathrm{m}}N_{\mathrm{f}}-N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}-2N_{\mathrm{m}}N_{\mathrm{f}}\varphi_{\mathrm{MF}}+(N_{\mathrm{m}}+N_{\mathrm{f}})\varphi_{\mathrm{MF}}+(N_{\mathrm{m}}+N_{\mathrm{f}})(\varphi_{\mathrm{MF}}+\varphi_{\mathrm{MM}})(N_{\mathrm{m}}-1)\right)}{(N_{\mathrm{m}}-\tilde{\varphi}_{\mathrm{MM}})(4N_{\mathrm{m}}N_{\mathrm{f}}-N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}}-N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}}-2N_{\mathrm{m}}N_{\mathrm{f}}\varphi_{\mathrm{MF}}+(N_{\mathrm{m}}+N_{\mathrm{f}})\varphi_{\mathrm{MF}})-\tilde{\varphi}_{\mathrm{MM}}(N_{\mathrm{m}}+N_{\mathrm{f}})(\varphi_{\mathrm{MF}}+\varphi_{\mathrm{MM}})(N_{\mathrm{m}}-1)}\,. \qquad [A2.34]$$

Setting $m_{\mathrm{m}} = m_{\mathrm{f}} = m$ and assuming that $N_{\mathrm{m}} = N_{\mathrm{f}} = N$ is large, thus neglecting terms of order $1/N^2$, these reduce to:

$$\frac{c_\omega}{b_\omega} < \frac{4x(1-m)^2\left(1+\frac{1}{2}\bar{a}\,\bar{\omega}(1-m)^2(s_\mathrm{f}-s_\mathrm{m})(1-s_\mathrm{f}-s_\mathrm{m})\right)}{N\left(1-(1-m)^2\left(1-2\bar{a}\,\bar{\omega}\,x(1-x)\right)\right)}, \qquad \text{[A2.35]}$$

where $x = 1 - (s_\mathrm{f} + s_\mathrm{m})/2$. Noting that $b_\omega = \bar{\omega}\, B_\omega / (1 - m_\mathrm{m})$ and $c_\omega = C_\omega$ in Lehmann and Feldman's (2008) notation, this recovers their result see (see equation (3.2) in Lehmann and Feldman (2009)).

When the phenotype is controlled by the genotype of the mother of the focal individual (p_s, $p_{\mathrm{male|mother}}$, $p_{\mathrm{female|mother}}$) the conditions are given by:

$$\frac{c_\omega}{b_\omega} < \frac{2(1-m_\mathrm{m})\left((1-s_\mathrm{m})(1-m_\mathrm{m})+(1-s_\mathrm{f})(1-m_\mathrm{f})\right)\left(4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}-2N_\mathrm{m}N_\mathrm{f}\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})(\varphi_\mathrm{MF}+\varphi_\mathrm{FF})(N_\mathrm{f}-1)\right)}{(N_\mathrm{f}-\tilde{\varphi}_\mathrm{MM})(4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}-2N_\mathrm{m}N_\mathrm{f}\varphi_\mathrm{MF}+(N_\mathrm{m}+N_\mathrm{f})\varphi_\mathrm{MF})-\tilde{\varphi}_\mathrm{MM}(N_\mathrm{m}+N_\mathrm{f})(\varphi_\mathrm{MF}+\varphi_\mathrm{FF})(N_\mathrm{f}-1)}. \qquad \text{[A2.36]}$$

When the genotype of the focal individual controls the phenotype (p_I, $p_{\mathrm{male|individual}}$, $p_{\mathrm{female|individual}}$) these is:

$$\frac{c_\omega}{b_\omega} < \frac{2(1-m_\mathrm{m})\left((1-s_\mathrm{m})(1-m_\mathrm{m})+(1-s_\mathrm{f})(1-m_\mathrm{f})\right)(N_\mathrm{f}+N_\mathrm{m})}{4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}-2N_\mathrm{m}N_\mathrm{f}\varphi_\mathrm{MF}-\tilde{\varphi}_\mathrm{MM}(N_\mathrm{m}+N_\mathrm{f})}. \qquad \text{[A2.37]}$$

Finally, granting full control over the phenotype to paternal-origin genes ($p_{\mathrm{I|paternal}}$, $p_{\mathrm{male|paternal}}$, $p_{\mathrm{female|paternal}}$) we have:

$$\frac{c_\omega}{b_\omega} < \frac{2(1-m_m)\left((1-s_\mathrm{m})(1-m_\mathrm{m})+(1-s_\mathrm{f})(1-m_\mathrm{f})\right)(4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}+(N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{m}-1)\varphi_\mathrm{MM}+N_\mathrm{m}(N_\mathrm{m}-N_\mathrm{f})\varphi_\mathrm{MF})}{N_\mathrm{m}(8N_\mathrm{f}N_\mathrm{m}-2N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-2N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}-4N_\mathrm{f}N_\mathrm{m}\varphi_\mathrm{MF})-\tilde{\varphi}_\mathrm{MM}(4N_\mathrm{f}N_\mathrm{m}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}+(N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{m}-1)\varphi_\mathrm{MM}+N_\mathrm{m}(N_\mathrm{m}-N_\mathrm{f})\varphi_\mathrm{MF})},$$

[A2.38]

and granting full control over the phenotype to paternal-origin genes ($p_{\mathrm{I|maternal}}$, $p_{\mathrm{male|maternal}}$, $p_{\mathrm{female|maternal}}$), we obtain:

$$\frac{c_\omega}{b_\omega} < \frac{2(1-m_\mathrm{m})\left((1-s_\mathrm{m})(1-m_\mathrm{m})+(1-s_\mathrm{f})(1-m_\mathrm{f})\right)(4N_\mathrm{m}N_\mathrm{f}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}+(N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{f}-1)\varphi_\mathrm{FF}+N_\mathrm{f}(N_\mathrm{f}-N_\mathrm{m})\varphi_\mathrm{MF})}{N_\mathrm{f}(8N_\mathrm{f}N_\mathrm{m}-2N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-2N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}-4N_\mathrm{f}N_\mathrm{m}\varphi_\mathrm{MF})-\tilde{\varphi}_\mathrm{MM}(4N_\mathrm{f}N_\mathrm{m}-N_\mathrm{f}(N_\mathrm{m}-1)\varphi_\mathrm{MM}-N_\mathrm{m}(N_\mathrm{f}-1)\varphi_\mathrm{FF}+(N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{f}-1)\varphi_\mathrm{FF}+N_\mathrm{f}(N_\mathrm{f}-N_\mathrm{m})\varphi_\mathrm{MF})}.$$

[A2.39]

INDIVIDUAL-BASED SIMULATIONS FOR BRAVERY EVOLUTION

We develop an individual-based simulation model of bravery evolution for the purpose of illustration and to assess the robustness of our analytical results. We consider a population of $p = 400$ groups, each containing $N_\mathrm{f} = 10$ adult females and $N_\mathrm{m} =10$ adult males. Each individual carries a bravery locus with two alleles, each of which is represented by a real-valued number, multiple of 0.02, lying between 0 and 1, including the extremes. At initialisation, all allele values are assigned a randomly-chosen allowed value. Each adult female produces $k = 100$ daughters and $k = 100$ sons, mating randomly each time, so that the offspring of the same mother do not always share the same father (absolute promiscuity). When each offspring is produced, each gene mutates with probability $M = 0.001$ to a new value, which can be, the current value the current value + 0.02, or the current value – 0.02, with equal probability. Subadult females migrate to a randomly-selected group with probability m_f; subadult males to a randomly-selected group probability m_m. Warfare is modelled as follows: for tractability, we imagine that all groups are arranged in a circle (at every generation the order of groups is randomised, to avoid neighbour effects); each group attacks the next one in the circle clockwise with a probability equal to the optimal belligerence value under individual control, as predicted by our analytical model (see Fig. 2a); the group wins the war with probability $\omega = 0.5(1 + \Omega_\mathrm{att} - \Omega_\mathrm{def})$, where Ω_att is the average bravery allelic value of subadult males in the attacking group and where Ω_def is the average bravery allelic value of subadult males in the defending group; each individual is assigned a competitiveness value in their own group (“home”), which depends on whether the group has been attacked and which group won, and a competitiveness value in the neighbouring group (“abroad”), which depends on whether the focal group has attacked that group and which group won (see Methods). During the following phase (density dependent regulation), $N_\mathrm{f} = 10$ females are randomly sampled (using competitiveness values as weights) to become adults; analogously $N_\mathrm{m} = 10$ males are randomly sampled (using competitiveness values as weights) to become adults. These then produce the next generation of subadults in the following cycle. We track $G = 10{,}000$ generations of evolution and calculate average allelic values of bravery in each generation. The data points shown in Figure A2.6 come from a single simulation and are the mean of the average allelic values of the last 1000 generations of evolution. The simulation code (*Wolfram Mathematica* file) is available online at: http://rspb.royalsocietypublishing.org/content/284/1849/20162699.figures-only.

Simulation results show a reasonable fit with our analytical predictions (Fig A2.6), given that evolutionary trajectories in the simulation model are influenced by random drift and spontaneous mutation. Simulation results are noisier than those for belligerence (Fig A5.3.1): this conforms to our expectation that stochastic effects would be stronger for bravery than for belligerence, because bravery is expressed only when a group is involved in a war. Secondly, simulation results are noisier under maternal and paternal control than under individual control: this conforms to our expectation that stochastic effects would be stronger under maternal and paternal control, because in these cases selection acts on a much smaller number of individuals (i.e. mothers or fathers, rather than subadults males themselves).

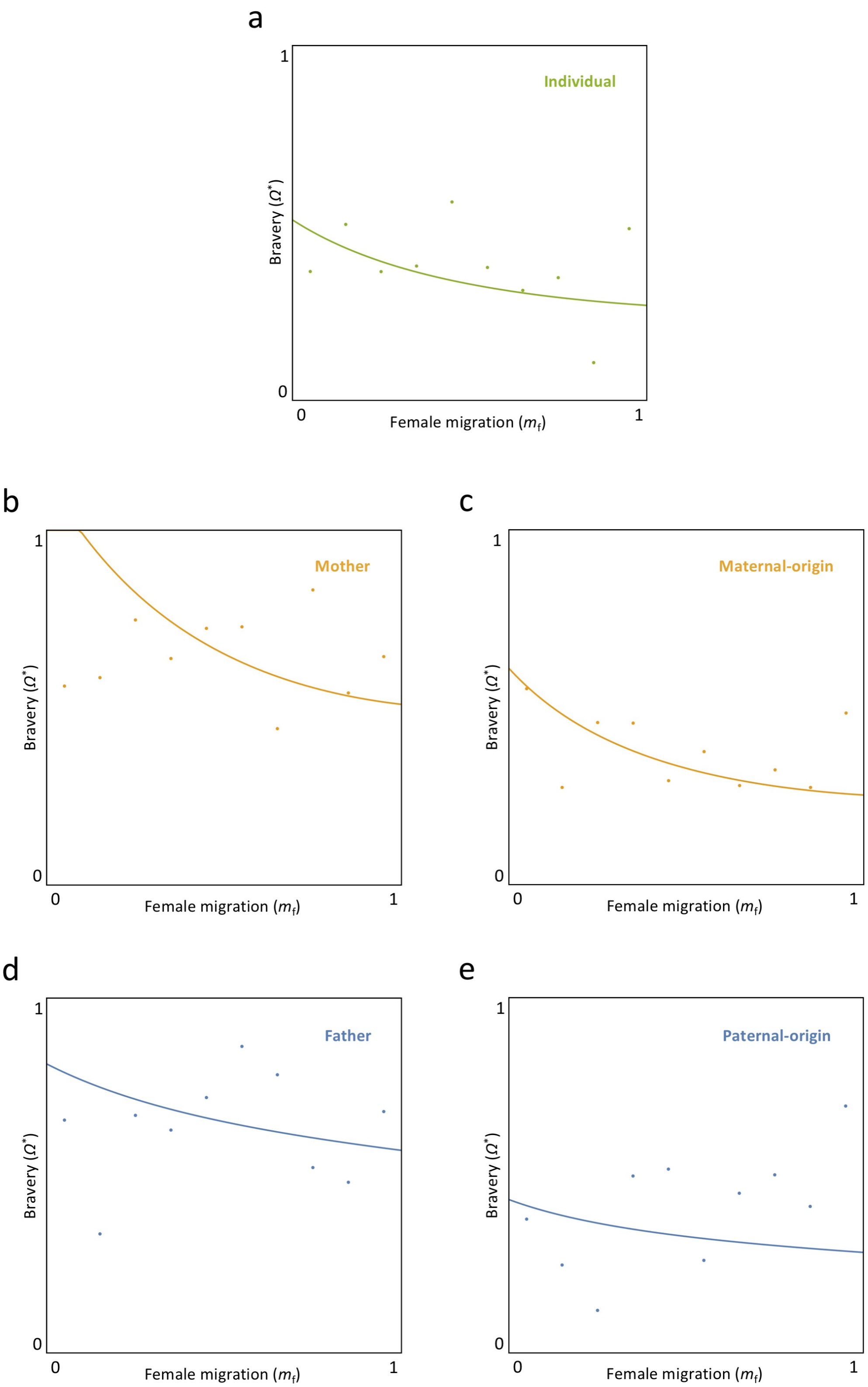

Figure A2.6 – Evolution of bravery. Analytical predictions (lines) and individual-based simulation results (filled circles) for convergence-stable levels of bravery (Ω^*) as a function of female migration (m_f) when bravery is controlled by the focal male (panel a), his mother (panel b), his father (panel d), his maternal-origin genes (panel c), or his paternal-origin genes (panel e). Other parameter values are $\bar{a} = A^*_{\text{ind}}$, $m_m = 0.5$, $s_f = 1$, $s_m = 0$, $N_f = N_m = 10$. We assume functional forms $\omega(\Omega_{\text{att}}, \Omega_{\text{def}}) = ½\,(1 + \Omega_{\text{att}} - \Omega_{\text{def}})$ and $\tau = 1 - 0.025\,\Omega^2$.

Table A2.1 – Coefficients of consanguinity and relatedness under focal individual control

SYMBOL VALUE

SYMBOL	VALUE
$\boldsymbol{p}_{\mathrm{I}}$	$\dfrac{8\,N_{\mathrm{f}}\,N_{\mathrm{m}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 4N_{\mathrm{f}}\,N_{\mathrm{m}}\,\varphi_{\mathrm{MF}}}{2(8\,N_{\mathrm{f}}\,N_{\mathrm{m}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - (4N_{\mathrm{f}}\,N_{\mathrm{m}} + N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{MF}})}$
$\boldsymbol{p}_{\mathbf{male\vert controller}}$	$(1-m_{\mathrm{m}})^2\,\dfrac{N_{\mathrm{f}} + N_{\mathrm{m}}}{8\,N_{\mathrm{f}}\,N_{\mathrm{m}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - (4N_{\mathrm{f}}\,N_{\mathrm{m}} + N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{MF}}}$
$\boldsymbol{p}_{\mathbf{female\vert controller}}$	$(1-m_{\mathrm{m}})(1-m_f)\,\dfrac{N_{\mathrm{f}} + N_{\mathrm{m}}}{8\,N_{\mathrm{f}}\,N_{\mathrm{m}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - (4N_{\mathrm{f}}\,N_{\mathrm{m}} + N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{MF}}}$
$\boldsymbol{R}_{\mathbf{male\vert controller}}$	$(1-m_{\mathrm{m}})^2\,\dfrac{2(N_{\mathrm{f}} + N_{\mathrm{m}})}{8\,N_{\mathrm{f}}\,N_{\mathrm{m}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 4N_{\mathrm{f}}\,N_{\mathrm{m}}\,\varphi_{\mathrm{MF}}}$
$\boldsymbol{R}_{\mathbf{female\vert controller}}$	$(1-m_{\mathrm{m}})(1-m_f)\,\dfrac{2(N_{\mathrm{f}} + N_{\mathrm{m}})}{8\,N_{\mathrm{f}}\,N_{\mathrm{m}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 4N_{\mathrm{f}}\,N_{\mathrm{m}}\,\varphi_{\mathrm{MF}}}$
	$N_{\mathrm{m}}\Big(\quad 4\,N_{\mathrm{f}}\,N_{\mathrm{m}} - N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 2N_{\mathrm{f}}\,N_{\mathrm{m}}\varphi_{\mathrm{MF}} + (N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{MF}} \quad\Big)$
$\boldsymbol{R}_{\mathbf{female\vert father}}$	$(1-m_{\mathrm{m}})(1-m_{\mathrm{f}})\,\dfrac{1}{N_{\mathrm{m}}}\left(\dfrac{4\,N_{\mathrm{f}}N_{\mathrm{m}} - N_{\mathrm{f}}(N_{\mathrm{m}}-1)\varphi_{\mathrm{MM}} - N_{\mathrm{m}}(N_{\mathrm{f}}-1)\varphi_{\mathrm{FF}} - 2N_{\mathrm{m}}N_{\mathrm{f}}\varphi_{\mathrm{MF}} + (N_{\mathrm{f}} + N_{\mathrm{m}})\varphi_{\mathrm{MF}} + (N_{\mathrm{m}}-1)(\varphi_{\mathrm{MF}} + \varphi_{\mathrm{MM}})(N_{\mathrm{f}} + N_{\mathrm{m}})}{4\,N_{\mathrm{f}}\,N_{\mathrm{m}} - N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 2N_{\mathrm{f}}\,N_{\mathrm{m}}\varphi_{\mathrm{MF}} + (N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{MF}}}\right)$
$\boldsymbol{R}_{\mathbf{male\vert mother}}$	$(1-m_{\mathrm{m}})^2\,\dfrac{1}{N_{\mathrm{f}}}\left(\dfrac{4\,N_{\mathrm{f}}\,N_{\mathrm{m}} - N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 2N_{\mathrm{m}}N_{\mathrm{f}}\varphi_{\mathrm{MF}} + (N_{\mathrm{f}} + N_{\mathrm{m}})\varphi_{\mathrm{MF}} + (N_{\mathrm{f}}-1)(\varphi_{\mathrm{MF}} + \varphi_{\mathrm{FF}})(N_{\mathrm{f}} + N_{\mathrm{m}})}{4\,N_{\mathrm{f}}\,N_{\mathrm{m}} - N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 2N_{\mathrm{f}}\,N_{\mathrm{m}}\varphi_{\mathrm{MF}} + (N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{MF}}}\right)$
$\boldsymbol{R}_{\mathbf{female\vert mother}}$	$(1-m_{\mathrm{m}})(1-m_{\mathrm{f}})\,\dfrac{1}{N_{\mathrm{f}}}\left(\dfrac{4\,N_{\mathrm{f}}\,N_{\mathrm{m}} - N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 2N_{\mathrm{m}}N_{\mathrm{f}}\varphi_{\mathrm{MF}} + (N_{\mathrm{f}} + N_{\mathrm{m}})\varphi_{\mathrm{MF}} + (N_{\mathrm{f}}-1)(\varphi_{\mathrm{MF}} + \varphi_{\mathrm{FF}})(N_{\mathrm{f}} + N_{\mathrm{m}})}{4\,N_{\mathrm{f}}\,N_{\mathrm{m}} - N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{MM}} - N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{FF}} - 2N_{\mathrm{f}}\,N_{\mathrm{m}}\varphi_{\mathrm{MF}} + (N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{MF}}}\right)$

Table A2.2 – Coefficients of consanguinity and relatedness under paternal- and maternal-origin genes control

SYMBOL	VALUE
$\boldsymbol{p}_{\mathbf{I}}, \boldsymbol{p}_{\mathbf{I\|paternal}}$ $\boldsymbol{p}_{\mathbf{I\|maternal}}$	$\frac{8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - 4N_\mathrm{f}\,N_\mathrm{m}\,\varphi_\mathrm{MF}}{2(8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - (4N_\mathrm{f}\,N_\mathrm{m} + N_\mathrm{m} + N_\mathrm{f})\varphi_\mathrm{MF})}$
$\boldsymbol{p}_{\mathbf{male\|paternal}}$	$(1-m_\mathrm{m})^2\,\frac{1}{N_\mathrm{m}}\left(\frac{4N_\mathrm{f}\,N_\mathrm{m} - N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} + (N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{m}-1)\varphi_\mathrm{MM} + N_\mathrm{m}(N_\mathrm{m}-N_\mathrm{f})\varphi_\mathrm{MF}}{2(8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - (4N_\mathrm{f}\,N_\mathrm{m} + N_\mathrm{m} + N_\mathrm{f})\varphi_\mathrm{MF})}\right)$
$\boldsymbol{p}_{\mathbf{female\|paternal}}$	$(1-m_\mathrm{m})(1-m_\mathrm{f})\frac{1}{N_\mathrm{m}}\left(\frac{4N_\mathrm{f}\,N_\mathrm{m} - N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} + (N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{m}-1)\varphi_\mathrm{MM} + N_\mathrm{m}(N_\mathrm{m}-N_\mathrm{f})\varphi_\mathrm{MF}}{2(8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - (4N_\mathrm{f}\,N_\mathrm{m} + N_\mathrm{m} + N_\mathrm{f})\varphi_\mathrm{MF})}\right)$
$\boldsymbol{p}_{\mathbf{male\|maternal}}$	$(1-m_\mathrm{m})^2\,\frac{1}{N_\mathrm{f}}\left(\frac{4N_\mathrm{f}\,N_\mathrm{m} - N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} + (N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{f}-1)\varphi_\mathrm{FF} + N_\mathrm{f}(N_\mathrm{f}-N_\mathrm{m})\varphi_\mathrm{MF}}{2(8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - (4N_\mathrm{f}\,N_\mathrm{m} + N_\mathrm{m} + N_\mathrm{f})\varphi_\mathrm{MF})}\right)$
$\boldsymbol{p}_{\mathbf{female\|maternal}}$	$(1-m_\mathrm{m})(1-m_\mathrm{f})\frac{1}{N_\mathrm{f}}\left(\frac{4N_\mathrm{f}\,N_\mathrm{m} - N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} + (N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{f}-1)\varphi_\mathrm{FF} + N_\mathrm{f}(N_\mathrm{f}-N_\mathrm{m})\varphi_\mathrm{MF}}{2(8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - (4N_\mathrm{f}\,N_\mathrm{m} + N_\mathrm{m} + N_\mathrm{f})\varphi_\mathrm{MF})}\right)$
$\boldsymbol{R}_{\mathbf{male\|paternal}}$	$(1-m_\mathrm{m})^2\,\frac{1}{N_\mathrm{m}}\left(\frac{4N_\mathrm{f}\,N_\mathrm{m} - N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} + (N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{m}-1)\varphi_\mathrm{MM} + N_\mathrm{m}(N_\mathrm{m}-N_\mathrm{f})\varphi_\mathrm{MF}}{8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - 4N_\mathrm{f}\,N_\mathrm{m}\,\varphi_\mathrm{MF}}\right)$
$\boldsymbol{R}_{\mathbf{female\|paternal}}$	$(1-m_\mathrm{m})(1-m_\mathrm{f})\frac{1}{N_\mathrm{m}}\left(\frac{4N_\mathrm{f}\,N_\mathrm{m} - N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} + (N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{m}-1)\varphi_\mathrm{MM} + N_\mathrm{m}(N_\mathrm{m}-N_\mathrm{f})\varphi_\mathrm{MF}}{8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - 4N_\mathrm{f}\,N_\mathrm{m}\,\varphi_\mathrm{MF}}\right)$
$\boldsymbol{R}_{\mathbf{male\|maternal}}$	$(1-m_\mathrm{m})^2\,\frac{1}{N_\mathrm{f}}\left(\frac{4N_\mathrm{f}\,N_\mathrm{m} - N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} + (N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{f}-1)\varphi_\mathrm{FF} + N_\mathrm{f}(N_\mathrm{f}-N_\mathrm{m})\varphi_\mathrm{MF}}{8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - 4N_\mathrm{f}\,N_\mathrm{m}\,\varphi_\mathrm{MF}}\right)$
$\boldsymbol{R}_{\mathbf{female\|\ maternal}}$	$(1-m_\mathrm{m})(1-m_\mathrm{f})\frac{1}{N_\mathrm{f}}\left(\frac{4N_\mathrm{f}\,N_\mathrm{m} - N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} + (N_\mathrm{f}+N_\mathrm{m})(N_\mathrm{f}-1)\varphi_\mathrm{FF} + N_\mathrm{f}(N_\mathrm{f}-N_\mathrm{m})\varphi_\mathrm{MF}}{8\,N_\mathrm{f}\,N_\mathrm{m} - 2N_\mathrm{f}(N_\mathrm{m}-1)\,\varphi_\mathrm{MM} - 2N_\mathrm{m}(N_\mathrm{f}-1)\,\varphi_\mathrm{FF} - 4N_\mathrm{f}\,N_\mathrm{m}\,\varphi_\mathrm{MF}}\right)$

3 Why war is a man's game‡

πόλεμος δ' ἄνδρεσσι μελήσει
War belongs to man

–Homer, *The Iliad*
(trans. W. Cowper)

Woolf's *Three Guineas* […] offered the originality […] of focusing on what was regarded as too obvious or inapposite to be mentioned, much less brooded over: that war is a man's game — that the killing machine has a gender, and it is male.

–Susan Sontag, *Regarding the Pain of Others*

Abstract

Interest in the evolutionary origins and drivers of warfare in ancient and contemporary small-scale human societies has greatly increased in the last decade, and has been particularly spurred by exciting archaeological discoveries that suggest that prehistoric humans led more violent lives than previously documented. However, the striking

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observation that warfare is an almost-exclusively male activity remains unexplained. Three general hypotheses have been proposed, concerning greater male effectiveness in warfare, lower male costs, and patrilocality. But while each of these factors might explain why warfare is more common in men, they do not convincingly explain why women almost never participate. Here, we develop a mathematical model to formally assess these hypotheses. Surprisingly, we find that exclusively-male warfare may evolve even in the absence of any such sex differences, though sex biases in these parameters can make this evolutionary outcome more likely. The qualitative observation that participation in warfare is almost-exclusive to one sex is ultimately explained by the fundamentally sex-specific nature of Darwinian competition – in fitness terms, men compete with men and women with women. These results reveal a potentially key role for ancestral conditions in shaping our species' patterns of sexual division of labour and violence-related adaptations and behavioural disorders.

Introduction

Recent contributions from multiple disciplines – including archaeology, psychology, evolutionary biology and anthropology – have greatly deepened our understanding of warfare, which may be broadly defined as coalitionary intergroup aggression (Kelly, 2005; Fry 2006, 2007; Gat, 2006; Choi and Bowles, 2007; Smirnov, et al., 2007; Lehmann and Feldman, 2008; Bowles, 2009; van Vugt, 2009; Pinker, 2011; Wrangham and Glowacki, 2012; Ferguson, 2013; Fry and Söderberg, 2013; Turchin, et al., 2013; Johnson and Toft, 2014; Glowacki and Wrangham, 2015; Low 2015; Turchin 2015; Zefferman and Mathew, 2015; Gómez, et al., 2016; Lopez, 2016; Nakao, et al., 2016; Micheletti, et al. 2017;

Chapter 2; Tescheler-Nicola, 2012; Wahl and Trautmann, 2012; Meyer, et al., 2015; Mirazón-Lahr, et al., 2016; Sala, et al., 2016). However, the extreme sex difference in individuals' involvement in warfare remains unexplained. In our evolutionary past, warfare was mainly – most likely, almost-exclusively – a male pursuit, as revealed by major discoveries of prehistoric mass graves and other material evidence of lethal intergroup conflict (Keeley, 1996; Osgood, et al., 2000; Teschler-Nicola, 2012; Meyer, et al., 2015; Mirazón-Lahr, et al., 2016). Similarly, in the vast majority of historical and contemporary hunter-gatherer and small-scale societies, women have only rarely participated in warfare in a direct way – i.e. in fighting – and their usual role, if any, has been a supporting one (Adams, 1983; Keeley, 1996; Wrangham and Peterson, 1997; Gat, 2000a, 2000b, 2000c, 2006; van Vugt, 2009; Low, 2015). This strong sex difference is also observed in chimpanzees, which are our closest living relatives and are understood to be the only other primates that routinely engage in lethal intergroup conflict (Manson and Wrangham, 1991; Wrangham, 1999; Wrangham and Glowacki 2012; the sister species of chimpanzees, bonobos, do not engage in violent intergroup conflict; Wilson, et al., 2014; Wrangham, 2018). On the face of it, this pattern is puzzling because, if likelihood of success in warfare increases with the size of the war party, it is unclear why more than half of a group's potential warriors would almost-always fail to participate in battle. The puzzle is not why male participation in warfare is more common than female participation (we outline potential explanations for this directly below), but why this imbalance is commonly so extreme, i.e. women taking no part at all.

Three general non-mutually exclusive hypotheses have been offered to explain this male bias in propensity to take part in warfare, and no general consensus has been reached.

First, men might be predisposed to warfare because they are better at it. Specifically, having greater weight, height and muscle mass may allow most men to perform more effectively in battle than most women (Gat, 2000c). Second, the net cost of warfare may be lower for men than women. In particular, whilst the fitness impact of risking death in battle may be significantly offset by a surviving warrior achieving great mating success, this is more likely to be true for men than for women owing to the way that male fitness can scale almost indefinitely with mating success while female fitness has natural limits (Bateman 1948; Low, 1993, 2015; Gat, 2000c; van Vugt, 2009). Also, the costs of participation in warfare are likely to be greater for women on account of the possibility of being pregnant or lactating, offspring survival being more strongly dependent on the continued presence of the mother than the father, sexual division of labour and central place foraging leading to the opportunity costs of travelling being greater for women (e.g. (Milner, et al., 2014)), and finally the risk of sexual coercion in case of defeat (Gat, 2000c; van Vugt, 2009; Scalise Sugiyama, 2014).

Third, women may be relatively less incentivized to participate in warfare owing to female-biased dispersal being associated with their having lower kinship to those groupmates who stand to benefit in the event of success in warfare (Manson and Wrangham, 1991; Low 1993). Female-biased dispersal has long been believed to characterise ancestral human populations living during the Pleistocene and Early Holocene (e.g. Ember, 1975, 1978; Foley, 1995; Wrangham and Peterson, 1996) but this view is now being debated and ancestral dispersal patterns are now an active area of research (Marlowe, 2005; Hill, et al, 2011; Sugiyama, 2017). Female-biased dispersal characterises other extant hominid species, chimpanzees, bonobos, gorillas (Lawson Handley and Perrin, 2007), in striking contradistinction to the usual mammalian syndrome of male-biased dispersal (Greenwood, 1980; Dobson, 1982) – suggesting that this pattern might have been dominant in ancestral humans too. However, population genetic studies have offered mixed results, with Seielstad, et al. (1998) finding evidence of genetic signatures of higher female than male dispersal in our ancestral past, and Wilder, et al. (2004) failing to find such a bias.

Evidence from the study of extant hunter-gatherer populations – whose lifestyle is considered to best approximate that of our Pleistocene ancestors (Marlowe, 2005) – is similarly mixed (and it is also difficult to interpret, as residence rules and sex biases in dispersal do not necessarily always coincide; see Ch.6, Box 6.2). Reviews of residence patterns in hunter gatherers that are now considered classic (Ember 1975, 1978) suggest that most hunter gatherers are virilocal, with women moving to the husband's household, resulting – at least to a certain extent – in a female bias in dispersal. More recent reviews highlight that hunter-gatherers are better described as 'multilocal', with different individuals adopting different strategies at different times during their lives, i.e. living with wife's relatives, with husband's relatives, or away from both (Marlowe, 2005; Hill, et al., 2011). Nonetheless, Hill, et al. (2011) find that in 17 hunter-gather societies (out of a sample of 32) there are more co-residing brothers than co-residing sisters, while only three societies show the opposite pattern.

To formally assess the feasibility of these three hypotheses, and to explore how readily they explain extreme sex-bias in participation in warfare – in terms of whether such sex differences are necessary and sufficient for exclusively-male warfare to evolve – we extend an existing kin-selection model of exclusively-male warfare (Lehmann and Feldman, 2008; Micheletti, et al., 2017; Ch. 2) to incorporate participation by both men and women. We assume an infinite, group-structured population in which individuals disperse between groups with sex-specific probabilities, and then engage in warfare against other groups, with individual and group participation in warfare influencing the likelihood of enjoying reproductive success in one's own group and also in defeated groups (see Methods and Extended Methods for details). We use this model to investigate how natural selection might act to favour or disfavour male and/or female participation in warfare in the presence and absence of the previously-hypothesized basic underlying sex differences. However, our key aim is to determine the conditions under which exclusively-male participation in warfare might be expected to emerge as a stable evolutionary outcome.

Methods

We adapt and expand an existing model of exclusively-male participation in warfare (Lehmann and Feldman, 2008; Micheletti, et al., 2017; Chapter 2) so as to allow consideration of participation by both sexes. Specifically, we consider two coevolving traits: the tendency for a man to participate in war – i.e. the probability of joining the war party during either attack or defence – which we term male participation (Ω_m), and the tendency for a woman to participate, which we term female participation (Ω_f). Here, "participation" is equivalent to the "bravery" behaviour described in the exclusively-male-warfare versions of the model (Lehmann and Feldman, 2008; Micheletti, et al., 2017; Chapter 2) (see Extended Methods for details). In the model, war is broadly construed so as to include, for example, surprise attacks as well as pitched battles. It is defined as an agonistic interaction between two groups, in which a subset of individuals of each group cooperate and coordinate to seize reproductive opportunities from the other group, as detailed below.

We consider an infinite population consisting of groups of N_i adults of sex $i \in \{m,f\}$. In the first step of the life cycle, each woman produces a large number K_i of sex-i offspring, who grow to become young adults (following Lehmann and Feldman (2008) and Micheletti, et al. (2017; Chapter 2), we assume non-overlapping generations, so that only young adult individuals – hereafter "individuals" – have the opportunity to migrate, fight and reproduce in each generation). Each sex-i individual migrates to a randomly-chosen group with probability m_i. In every generation, each post-migration group can attack one randomly-chosen group, with probability a, and can be attacked by one other group, with the same probability a. If a war is initiated, a war party is formed in each of the two groups: each sex-i individual joins with probability Ω_i. The attacking group wins with probability $\omega(\Omega_{m,att}, \Omega_{f,att}, \Omega_{m,def}, \Omega_{f,def})$, where $\Omega_{i,att}$, and $\Omega_{i,def}$ are the average probabilities of participation of sex-i individuals in the attacking and defending groups, respectively; and $\partial\omega\left(\Omega_{m,att}, \Omega_{f,att}, \Omega_{m,def}, \Omega_{f,def}\right)/\partial\Omega_{i,att} = b_i$ is the marginal increase in the probability of the attacking group winning, contributed by participation of sex $i \in \{m,f\}$ (we assume that participation has equal importance in defence: $\partial\omega\left(\Omega_{m,att}, \Omega_{f,att}, \Omega_{m,def}, \Omega_{f,def}\right)/\partial\Omega_{i,def} = -b_i$). Density dependent competition follows warfare. In groups that were not attacked, individuals compete for reproductive opportunities against groupmates of the same sex; in groups that were attacked and successfully defended, individuals compete for reproductive opportunities against groupmates of the same sex, with sex-i individuals having competitiveness $\tau_i(\Omega_{i,ind})$ – where $\Omega_{i,ind}$ is the probability of participation of a sex-i individual, and $-(\partial\tau_i(\Omega_{i,ind})/\partial\Omega_{i,ind})/\tau_i(\overline{\Omega}_i) = c_i$ is the competitive cost of participation for an individual of sex i; and in defeated groups, individuals compete for reproductive opportunities against groupmates and attackers of the same sex, with sex-i individuals having competitiveness $\tau_{\mathrm{i}}(\Omega_{\mathrm{i,ind}}) \cdot s_{\mathrm{i}}$, if they belong to the defeated group, and $\tau_{\mathrm{i}}\left(\Omega_{\mathrm{i,ind}}\right) \cdot (1 - s_{\mathrm{i}})$, if they belong to the winning group. Notice that participation comes into play and incurs a competitive cost only when a group in involved in a war, either because it attacks or is attacked by another group. We perform a kin-selection analysis (Hamilton, 1964; Maynard Smith, 1964; Taylor, 1996; Taylor and Frank, 1996; Frank, 1997, 1998; Rousset, 2004; Taylor, et al., 2007) to determine how selection acts upon male participation and female participation in warfare (see Extended Methods for details).

Results

Analysing our model, we find that natural selection – including both direct and indirect (i.e. kin selection) effects (Hamilton, 1964; Maynard Smith, 1964; Taylor, 1996; Taylor and Frank, 1996; Frank, 1997, 1998; Rousset, 2004; Taylor, et al., 2007) – favours an increase in participation in warfare by an individual of sex i when:

$$-c_{\mathrm{i}} + \left(1 - 2\bar{\omega} s_{\mathrm{i}}(1 - s_{\mathrm{i}})\right) c_{\mathrm{i}} r_{\mathrm{ii}} + 2\left((1 - s_{\mathrm{i}}) r_{\mathrm{ii}} + \left(1 - s_{\mathrm{j}}\right) r_{\mathrm{ij}}\right) b_{\mathrm{i}} > 0, \qquad [3.1]$$

where c_{i} is the marginal cost of participation for that individual, b_{i} is the marginal increase in the probability of their group's victory, $\bar{\omega}$ is the population-average probability of an attacking group being victorious, s_{i} is the proportion of children born into defeated groups whose sex-i parent was a member of the defeated – rather than a winning – group, r_{ii} is the genetic relatedness of same-sex groupmates and r_{ij} is the relatedness of opposite-sex groupmates (both being lower than relatedness to self, which generates a collective action problem with tension between individual versus group interests). That is, by participating in warfare, an individual of sex i incurs: a direct-fitness cost (first term in condition [3.1]), owing to a loss $-c_{\mathrm{i}}$ of reproductive opportunities; an indirect-fitness benefit (second term), owing to a corresponding increase c_{i} of reproductive opportunities for other same-sex individuals, who are groupmates with probability $(1-2\bar{\omega}s_{\mathrm{i}}(1-s_{\mathrm{i}}))c_{\mathrm{i}}$ and in which case are related by r_{ii}; and an indirect-fitness benefit (third term), from improving the group's success in warfare by b_{i} and consequently increasing the reproductive success of same-sex groupmates – who are related by r_{ii} – by a factor $1-s_{\mathrm{i}}$ and that of opposite-sex groupmates – who are related by r_{ij} – by a factor $1-s_{\mathrm{j}}$. Note that condition [3.1] holds even when individuals gain a direct fitness benefit from participating ($c_{\mathrm{i}}<0$; see Extended Methods for details), such as high prestige leading to increased mating success or other fitness-enhancing benefits (Glowacki and Wrangham, 2015; Low, 2015), and may thus be satisfied even when groupmates are not genetically related.

In order to explore whether underlying sex differences are necessary for driving the evolution of single-sex participation, or whether this might occur for more basic reasons, we investigate the behaviour of our model in the simple, hypothetical case where these sex differences are absent. Consideration of condition [3.1] reveals that, even if there is no sex bias in any parameter and initially-equal participation of both sexes in warfare ($c_{\mathrm{m}} = c_{\mathrm{f}} = c$, $b_{\mathrm{m}} = b_{\mathrm{f}} = b$, $m_{\mathrm{m}} = m_{\mathrm{f}} = m$, $s_{\mathrm{m}} = s_{\mathrm{f}} = s$), evolution may nevertheless result in single-sex participation in warfare, on account of a feedback that occurs within each sex. Specifically, the direct cost of participation in warfare manifests as a reduction in competitiveness against same-sex individuals for reproductive opportunities, and we find that if this marginal cost increases with increasing level of participation by members of one's own sex ("accelerating cost"; $\partial c_{\mathrm{i}}/\partial \bar{\Omega}_{\mathrm{i}} > 0$, where $\bar{\Omega}_{\mathrm{i}}$ is the average level of participation in warfare by individuals of sex i), then the two sexes are favoured to participate equally (Fig. 3.1a). As an example of a scenario in which costs are accelerating, consider that there might be productive activities in the home group that influence competitiveness and require labourers, and these activities are carried out by one sex or the other, i.e. sexual division of labour (cf. Bliege Bird, 1999; Marlowe, 2007).

On the other hand, if the marginal cost of participation decreases with increasing level of participation by members of one's own sex ("decelerating cost"; $\partial c_{\mathrm{i}}/\partial \bar{\Omega}_{\mathrm{i}} < 0$; for example because an individual that participates in warfare is less likely to be cuckolded by a groupmate the more same-sex groupmates participate), then single-sex participation is favoured (Fig. 3.1b). If constraints prevent a favoured increase in participation from one sex from being evolutionarily realized – for example, if that sex is already fully participating in warfare – then this may lead to the other sex also participating in warfare in compensation. Hence, if the cost of participation is decelerating, any initial symmetry-breaking sex bias in participation is expected to become evolutionarily magnified, such that whether the population evolves male-only or female-only participation depends only on the initial conditions (i.e. "hysteresis").

This result reveals a fundamental role for sex in modulating selection pressures in relation to warfare such that – even in the absence of any other sex differences – the incentive for an individual to join a war party depends not only on how much other individuals are participating, but also on the individual's own sex and the sex of those other participating individuals. Specifically, an increased level of participation in warfare by sex-i individuals increases the incentive of a focal individual of the same sex to join the war party if

$$4(1-s)r\frac{\partial b_{\mathrm{i}}}{\partial \bar{\Omega}_{\mathrm{i}}}-\big(1-\big(1-2\bar{\omega}s(1-s)\big)r\big)\frac{\partial c_{\mathrm{i}}}{\partial \bar{\Omega}_{\mathrm{i}}}>0\ , \qquad [3.2]$$

whereas it increases the incentive of a focal individual of the other sex to join the war party if:

$$4(1-s)r\frac{\partial b_{\mathrm{j}}}{\partial \bar{\Omega}_{\mathrm{i}}}>0 \qquad [3.3]$$

(see Extended Methods for details). In particular: if cost is accelerating ($\partial c_{\mathrm{i}}/\partial \bar{\Omega}_{\mathrm{i}} > 0$), then the focal individual is relatively disincentivised to participate in warfare when same-sex individuals are already participating, leading to equal participation by both sexes being favoured (Fig. 3.1a); and if cost is decelerating ($\partial c_{\mathrm{i}}/\partial \bar{\Omega}_{\mathrm{i}} < 0$), then the focal individual is relatively incentivized to participate in warfare when same-sex individuals are already participating, leading to only one sex being favoured to participate in warfare (Fig. 3.1b).

These results explain why participation in warfare may involve one sex only, but not why participation in warfare is an exclusively-male rather than exclusively-female behaviour. To address this issue, we examine condition [3.1] to assess whether sex-differences in various underlying parameters may bias this evolutionary exaggeration towards exclusively-male participation rather than exclusively-female participation. In support of the aforementioned hypotheses, we find that certain sex-differences may result in a greater number of men than women participating in warfare (see Extended Methods for details). Moreover, we find that these sex differences may act in conjunction with the hysteresis effect described above to drive the evolution of exclusively-male war parties, with no women participating. Specifically, the basin of attraction for male-only

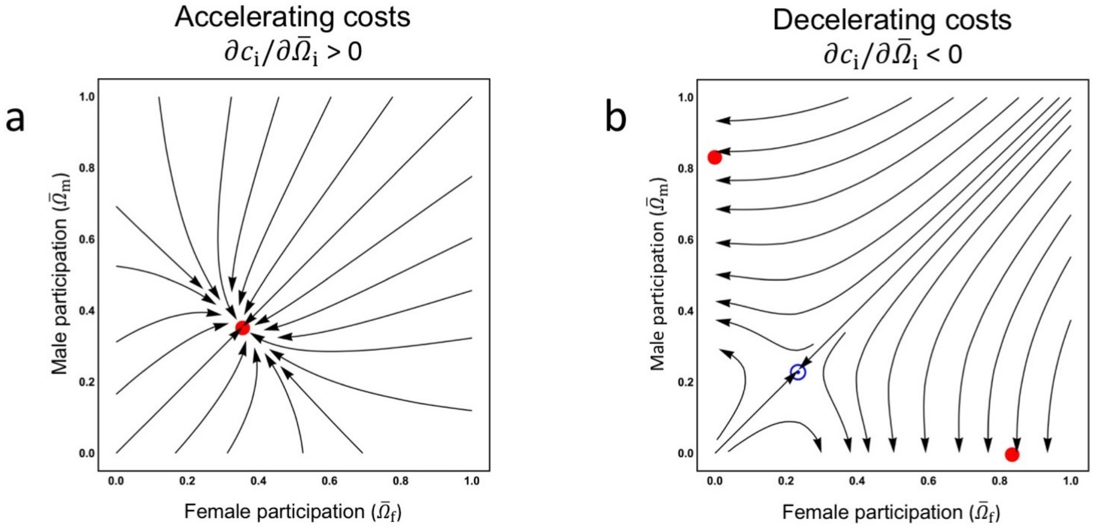

Figure 3.1 - Evolution of male and female participation in the absence of other sex differences in the ecology of war. Streamline plots showing the evolution of male and female participation in warfare ($\bar{\Omega}_m, \bar{\Omega}_f$) with accelerating personal costs (panel a) and with decelerating personal costs (panel b). Filled red circles represent stable equilibria and circled blue dots represent unstable equilibria. For the purposes of illustration, we assume competitiveness functional forms $\tau_{\mathrm{i}} = 1 - \chi_{\mathrm{i}}\, \Omega_{\mathrm{i}}^2$ (panel a), and $\tau_{\mathrm{i}} = 1 - \chi_{\mathrm{i}}\, \Omega_{\mathrm{i}}^{1/2}$ (panel b), and a symmetrical war outcome function $\omega(\sigma_{\mathrm{att}}, \sigma_{\mathrm{def}}) = \sigma_{\mathrm{att}} / (\sigma_{\mathrm{att}} + \sigma_{\mathrm{def}})$, where $\sigma_{\mathrm{att}} = ½ (\psi_{\mathrm{m}}\, \Omega_{\mathrm{m,att}} + \psi_{\mathrm{f}}\, \Omega_{\mathrm{f,att}})$ and $\sigma_{\mathrm{def}} = ½ (\psi_{\mathrm{m}}\, \Omega_{\mathrm{m,def}} + \psi_{\mathrm{f}}\, \Omega_{\mathrm{f,def}})$ are the fighting strengths of the attacker and the defender, respectively (see Extended Methods for details), with $\psi_{\mathrm{f}} = \psi_{\mathrm{m}} = 1$ and $\chi_{\mathrm{f}} = \chi_{\mathrm{m}} = 0.12$. Other parameter values are $\overline{\omega} = 0.5$, $\overline{a} = 1$, $N_{\mathrm{f}} = N_{\mathrm{m}} = 10$,
$m_{\mathrm{m}} = m_{\mathrm{f}} = 0.5$, $s_{\mathrm{f}} = s_{\mathrm{m}} = 0.15$.

participation is larger than that for female-only participation if men are more effective than women in war ($b_m > b_f$; Fig. 3.2a), if the cost of warfare is less for men than for women ($c_m < c_f$; Fig. 3.2b) or if women disperse at a greater rate than do men (resulting in women being less related to same-sex groupmates than men, $r_{ff} < r_{mm}$; Fig. 3.2c). In each of these scenarios the left-hand side of condition [3.1] is larger for men than for women, tilting participation in their favour and making this outcome more likely (see Extended Methods for details). That is, starting from initially unbiased participation (for example, no participation by either sex), the population is expected to embark on an evolutionary trajectory that ultimately results in exclusively-male warfare

Moreover, we identify a further sex difference that may make exclusively-male warfare more likely than exclusively-female warfare. This obtains when the mothers of children born into a defeated group represent a mixture of women from winning and defeated groups ("maternal admixture"; Micheletti, et al, 2017; Chapter 2)) to an extent that is greater than for the fathers ("paternal admixture"; Micheletti, et al, 2017; Chapter 2) of these children ($s_f(1 - s_f) > s_m(1 - s_m)$). This occurs, for example, when all men in defeated groups are killed and father no further children ($s_m = 0$) but some of the women are spared and go on to produce children ($0 < s_f < 1$). In such scenarios, a man who loses reproductive opportunities by participating in warfare is relatively more likely to reduce competition for reproductive opportunities among his male groupmates, from which he may derive an indirect-fitness benefit, but a woman who loses reproductive opportunities by participating in warfare is relatively more likely to reduce competition among unrelated women in other groups. Accordingly, the left-hand side of condition [3.1] is larger for men than it is for women and, accordingly, the basin of attraction for male-only participation is larger than that for female-only participation (Fig. 3.2d). Again, this means that a population that initially exhibits unbiased participation is expected to evolve to a condition of exclusively-male warfare.

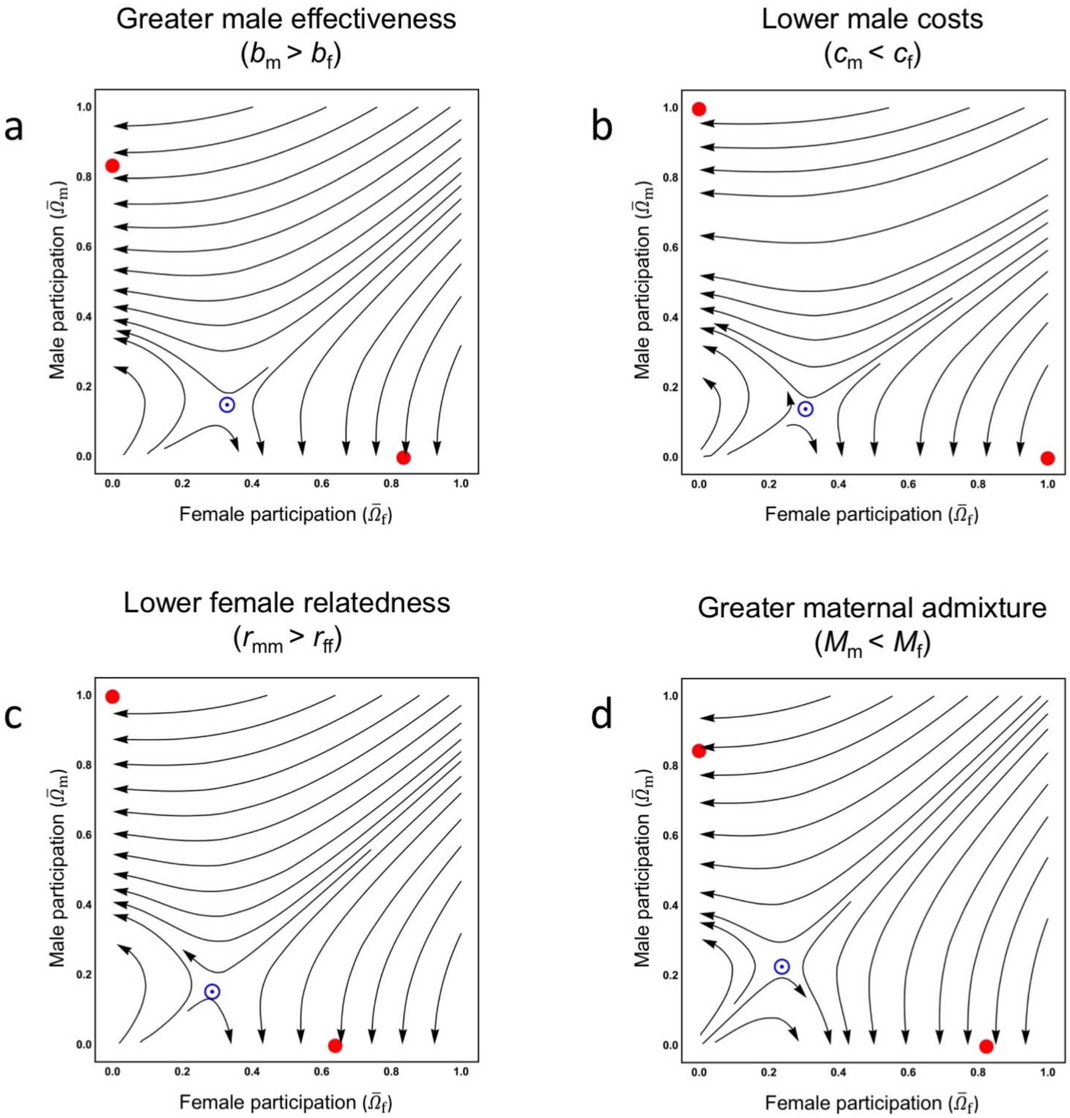

Figure 3.2 - Evolution of male and female participation in the context of other sex differences in the ecology of war. Streamline plots showing the evolution of male and female participation in warfare ($\bar{\Omega}_m, \bar{\Omega}_f$) when personal costs are decelerating and: effectiveness is greater for men than for women ($b_m > b_f$; panel a); men suffer lower personal costs than women ($c_m < c_f$; panel b); women are less related to their same-sex groupmates than men ($r_{mm} > r_{ff}$; panel c) as a result of female-biased dispersal; maternal admixture is greater than paternal admixture ($M_m < M_f$; panel d). Filled red circles represent stable equilibria and circled blue dots represent unstable equilibria. For the purposes of illustration, we assume a competitiveness functional form $\tau_i = 1 - \chi_i\, \Omega_i^{1/2}$, and a symmetrical war outcome function $\omega(\sigma_{att}, \sigma_{def}) = \sigma_{att} / (\sigma_{att} + \sigma_{def})$, where $\sigma_{att} = ½\, (\psi_m\, \Omega_{m,att} + \psi_f\, \Omega_{f,att})$ and $\sigma_{def} = ½\, (\psi_m\, \Omega_{m,def} + \psi_f\, \Omega_{f,def})$ are the fighting strengths of the attacker and the defender, respectively (see Extended Methods for details). Other parameter values are $\bar{\omega} = 0.5$, $\bar{a} = 1$, $N_f = N_m = 10$, $\psi_f = \psi_m = 1$ (except panel a: $\psi_f = 0.7$, $\psi_m = 1$), $\chi_f = \chi_m = 0.12$ (except panel b: $\chi_f = 0.14$, $\chi_m = 0.1$), $m_f = m_m = 0.2$ (except panel c: $m_f = 0.3$, $m_m = 0.1$), $s_f = s_m = 0.15$ (except panel d: $s_f = 0.3$, $s_m = 0$).

Discussion

Our primary aim was to explore why human warfare has been not just a predominantly male activity but a near-exclusively male activity. To address this question, we developed and analysed a model of the coevolution of male and female participation in warfare. Taken together, our results suggest an entirely novel explanation for why women do not participate in warfare. Archaeological, ethnographic and historical evidence overwhelmingly show that warfare was an almost-exclusively male activity in prehistoric societies (Keeley, 1996; Osgood, et al., 2000;Teschler-Nicola, 2012; Meyer, et al., 2015; Mirazón-Lahr, et al., 2016) and continued to be so in historical times in both small-scale societies and states throughout the ancient and modern world (Adams, 1983; Keeley, 1996; Wrangham and Peterson, 1997; Gat, 2000a, 2000b, 2000c, 2006; van Vugt, 2009; Low, 2015). Although women fought occasionally in North-American and Melanesian tribes (Gat, 2000a), in Scythian and Sarmatian steppe pastoralists – who may be linked to the Greek myth of the Amazons (Gat, 2000c) – in the African Kingdom of Dahomey (Goldschmidt, 1988), and in Viking raiding parties (Hedenstierna-Jonson, et al., 2017), there is no evidence of war being a predominantly or exclusively female activity in any human society. We have shown that this pattern may be explained by an evolutionary feedback between male and female participation in warfare – specifically, increased participation of one sex incentivising the same sex and disincentivising the other – revealing that sex itself is a fundamental modulator of involvement in intergroup conflict. This effect ultimately owes to the way in which competition for Darwinian fitness is only between individuals of the same sex, and hence is not specific to our model but applies over a wide range of assumed societal organizations, generational differences and migration patterns.

Considering only for illustration a simple hypothetical case with no sex difference in any underlying parameter (i.e. males and females are equally effective in war, pay equal costs of participation in war, gain equal direct benefits and indirect benefits to groupmates, and migrate with equal rates), the evolution of male-only participation requires only two conditions be met: (i) that personal costs decelerate with increasing participation of individuals of the same sex; and (ii) that there is an initial symmetry-breaking male bias in participation. As an example of a scenario leading to condition (i) being satisfied, consider that a man who leaves the group to participate in warfare is less likely to be cuckolded by a groupmate if his groupmates are also participating in warfare. Let us now consider a potential scenario that would lead to condition (ii) being met. If warfare's origins lay in within-group aggression occasionally spilling out to the between-group level, then any pre-existing male-bias in aggression – driven, for example, by standard sexual selection (Andersson, 1994) – would have provided such an initial symmetry-breaking and thus ensure subsequently-evolving warfare behaviours were exclusively-male in their expression. Thus, the empirically-observed pattern of warfare being not just male-biased but, in most cases, an exclusively-male activity, can be explained under a very generally-applicable set of circumstances.

Let us digress slightly to extend the line of reasoning related to warfare potentially having roots in within-group aggression. Warfare might therefore be conceptualized as a social innovation that allows wasteful sexually-selected conflict among male groupmates to be cooperatively redirected towards men in other groups, to the advantage of all group members. Beyond warfare, sexual feedbacks similar to those explored here may have played a role in the context of other group-beneficial social behaviours, such as communal care of infants and hunting, and might therefore explain striking patterns of sexual division of labour in human societies (Bliege Bird, 1999; Marlowe, 2007).

Returning to our key aim of explaining why warfare is not just a predominantly male activity, but in most cases exclusively-male: we have shown that, while they are not required for exclusively-male warfare to evolve, any of a number of underlying sex differences may make this outcome more likely, by enlarging its basin of attraction, such that it encompasses initial conditions in which both sexes participate equally (including neither sex participating at all). Three such sex differences have previously been articulated in the literature. First, greater male than female effectiveness in warfare may result in a man having a greater positive impact on the probability of winning the war and a correspondingly greater increase in the reproductive success of his groupmates than would a woman – in line with the rationale presented by Gat (2000c). Second, lower costs for men than women make male-only participation more likely, as suggested by Low (1993, 2015), Gat (2000c) and van Vugt (2009). Third, female-biased dispersal (patrilocality) increases the likelihood of male-only participation in two ways: it results in the indirect-fitness benefit accrued by men via increased breeding success for their groupmates being greater for men than for women, as suggested by Manson & Wrangham (1991) and Low (1993); and it also results in greater relaxation of kin competition for men than for women. As well as these three previously-posited factors, our analysis suggests a further one that has previously been neglected: greater maternal than paternal admixture results in participation in warfare relaxing kin competition among men more than among women, thus making male-only participation more likely (for a similar effect driving sex-biased dispersal, see Micheletti, et al., 2017; Chapter 2).

Low (1993, 2015) and Adams (1983) have argued that whilst such underlying sex differences may drive a male-bias in participation in warfare, they fail to convincingly explain why warfare is almost exclusively a male activity. Indeed, it was this criticism that was a spur for our investigations. Our analysis confirms this point: although each of these underlying factors may induce a quantitative male-bias in participation in warfare, we find that the qualitative observation that participants in warfare are almost exclusively male is ultimately explained by the fundamentally sex-specific nature of Darwinian competition in sexual populations (men compete with men, and women with women). That is, although it has been suspected that underlying sex differences might not be sufficient to explain the evolution of exclusively-male warfare, our analysis has shown that such sex differences are not even necessary.

How could this insight be tested empirically and the relative importance of hysteresis and sex differences in various parameters be assessed? An empirical study of the change in patterns of participation in warfare – or lack thereof – in various human populations that underwent ecological changes (e.g. in dispersal patterns) could offer perhaps a weak test. Because of hysteresis, we would not expect participation in warfare to become almost-exclusively female in those populations that have shifted to male-biased dispersal. Finding that they had would lend support to the idea that sex bias in dispersal is the key driver and hysteresis effects are weak. The lack of reports of societies where female participation is dominant suggests that hysteresis might be a more important factor, but a full assessment of this would require a detailed empirical study, which is beyond the scope of the present chapter.

The results of our model may also be applicable beyond humans. There is much controversy over the definition of warfare and, accordingly, as to which species should be regarded as exhibiting warfare behaviours (Wrangham, 1999; Bowles, 2009; Fry and Söderberg, 2013). However, the only vertebrates to have been observed to regularly engage in lethal conflict between conspecific groups are chimpanzees, spotted hyenas, wolves and lions (Wrangham, 1999). Our results offer a novel explanation for why, in chimpanzees, both attackers and victims are almost-always male (Wrangham and Peterson, 1997; Wrangham 1999; Wrangham and Glowacki, 2012), and suggest that male philopatry – generally considered to be crucial in determining this pattern (Manson and Wrangham, 1991) – may simply be a reinforcing factor (along with other sex differences, such as in ranging patterns (Pusey and Schroepfer-Walker, 2013)). In spotted hyenas, only females participate in raids against other groups (Wrangham, 1999; Boydston, et al., 2001), and this suggests that the sexual feedbacks occurring in our model may apply in this case such that an initial female bias (e.g. in aggressiveness) might have led to female-only participation. Conversely, in wolves and lions, both sexes appear to take part in intergroup raids (though not necessarily in equal numbers; Wrangham, 1999; Packer and Mosser, 2009; Cassidy, et al., 2015) which, in light of our analysis, suggests that personal costs might accelerate – rather than decelerate – with participation in these species. Finally, coalitionary killing is relatively common in many eusocial insects but, as their social systems (e.g. involving non-reproductive castes) and the modes and aims of their conflicts (e.g. attacking or defending against heterospecifics; Thorne, 1997; Chapman, et al., 2000; Hölldobler and Wilson, 2000;

Grüter, et al., 2012) are fundamentally different from those considered in our analysis, it is not clear that our results would be applicable to those systems.

Returning to our own species, in addition to explaining the evolutionary origins of exclusively-male warfare, our analysis may illuminate the biology of societally-damaging violence-related pathologies in contemporary populations. Crespi and Badcock (2008) have suggested that mutations and epimutations at loci controlling adaptive aggression behaviours may be linked with severe, psychotic-spectrum disorders, owing to the destabilizing effects of intragenomic conflict between an individual's maternal-origin versus paternal-origin genes, and Faria, et al. (2017) have pointed out that, if adaptive aggression behaviours are sex-limited in their expression, then concomitant violence disorders are also expected to be sex-limited, perhaps explaining their higher incidence in men than in women. Crespi & Badcock (2008) assumed that aggression is primarily a selfish, group-detrimental behaviour and, on that basis, predicted that psychotic-spectrum disorders are likely to be induced by deleterious mutations inherited from the individual's mother. However, if aggression has been primarily a selfless, group-beneficial behaviour – as in the case of participation in intergroup warfare – then the opposite pattern of parent-of-origin-specific expression is expected (Micheletti, et al., 2017; Chapter 2). Moreover, the present analysis underlines why such pathologies may be male-biased in their incidence, i.e. owing to our species' almost exclusively-male participation in warfare.

Finally, our results may help illuminate the evolutionary trajectories of warfare as societies have changed and polities become larger. Specifically, the presence of hysteresis – i.e. dependence on initial conditions and subsequent historical dynamics – might mean that, after an evolutionary equilibrium corresponding to a given set of initial biological and ecological conditions has been reached, the population is unlikely to move from that state, even if the conditions subsequently change. For example, in a society with male-only participation in warfare – which ancestrally had lower costs for men, female-biased migration and/or greater male effectiveness – almost-exclusively male involvement in warfare is likely to persist even if evolutionary innovations abolish sex differences in costs, effectiveness and rates of migration. This might explain why war is almost-exclusively the domain of men even in societies characterized by monogamy (in which there is less scope for men to enjoy limitless mating success) and in matrilocal, duolocal and neolocal populations in which dispersal is not female biased (e.g. Tibetan small-scale societies; Wu, et al., 2013; Ji, et al., 2016). In addition, it suggests an explanation for why women did not participate more in warfare with the introduction of weapons that appear to decrease male advantage, such as the bow and arrow (Adams, 1983; Gat, 2000c; Turchin, 2015). Similarly, the observation that in contemporary industrialized societies women's involvement in the armed forces is still considerably limited – though firepower and digitalisation have, in many ways, equalized the sexes in terms of effectiveness in warfare (Gat, 2000c) – need not be entirely due to cultural or ideological reasons, but might simply be a consequence of how ecological conditions our conspecifics faced in our remote past have shaped our biology. These patterns might nonetheless be altered, even very substantially, by the action of culture, cultural norms, and institutions – as exemplified by universal female conscription in Israel or the rising involvement of women in armed forces in numerous countries around the world (Simpson, 2016).

Extended methods

Preamble

Here, we adapt an existing kin-selection model of exclusively-male warfare (Lehmann and Feldman, 2008; Micheletti, et al., 2017; Chapter 2) to incorporate participation in warfare by both men and women. Specifically, we conceptualize the "bravery" trait – which in the studies by Lehmann and Feldman (2008) and Micheletti, et al., (2017; Chapter 2) measures the investment in warfare of a given individual – as the probability that that individual joins the war party when the group is involved in a war, and we term this trait "probability of participation" or "participation" in short. We consider the evolution of two traits: male participation, which is exhibited only by men, and female participation, which is exhibited only by women.

Fitness

Firstly, we derive the fitness of a focal young adult of sex i $\in\{m,f\}$, in a focal group, following the life cycle described in Methods. With probability $1 - m_i$, the focal young adult of sex-i does not migrate from the focal group. In every generation, each post-migration group can attack one randomly-chosen group. With probability $1 - a$, the focal group is not attacked by the other group and in this case the focal sex-i young adult competes for N_i breeding spots with $N_f K_i$ sex-i young adults (a fraction $1 - m_i$ of which originated from the focal group and a fraction m_i migrated from another group and in this way the migration terms cancel out; N_f is adult females) such that their probability of securing a breeding spot is $N_i/(N_f K_i)$. Alternatively, with probability a, the focal group is attacked and the attacking group loses the war with probability $1 - \omega''$, where $\omega'' \equiv \omega(\bar{\Omega}_m, \bar{\Omega}_f, \Omega_m', \Omega_f')$, $\bar{\Omega}_i$ is the average level of sex-i participation of the attacking group, and Ω_i' is the average level of sex-i participation of the focal group. In this case, the probability of obtaining reproductive success for a random sex-i young adult in the group must be corrected by $\tau_i(\Omega_i')$ and that of the focal sex-i young adult by $\tau_i(\Omega_i)$, where $\tau_i(\Omega_{i,ind})$ is sex-i competitiveness due to sex-i participation (with $d\tau_i/d\Omega_{i,ind} < 0$, and $\tau_i(0) = 1$), meaning that the focal sex-i young adult obtains a breeding spot with probability $N_\mathrm{i}\tau_\mathrm{i}(\Omega_\mathrm{i})/(N_\mathrm{f}K_\mathrm{i}\tau_\mathrm{i}(\Omega_\mathrm{i}'))$. Otherwise, the attacking group wins the war with probability ω''. In this case the focal sex-i young adult competes for $N_\mathrm{i}s_\mathrm{i}$ breeding spots with $N_\mathrm{f}K_\mathrm{i}s_\mathrm{i}$ sex-i young adults from their group and $N_\mathrm{f}K_\mathrm{i}(1 - s_\mathrm{i})$ sex-i young adult from the attacking group. Thus, adding the appropriate competitiveness modifiers, the focal sex-i young adult obtains a breeding spot with probability $N_\mathrm{i}\tau_\mathrm{i}(\Omega_\mathrm{i})s_\mathrm{i}/(N_\mathrm{f}K_\mathrm{i}\tau_\mathrm{i}(\Omega_\mathrm{i}')s_\mathrm{i}+ N_\mathrm{f}K_\mathrm{i}\tau_\mathrm{i}(\bar{\Omega}_\mathrm{i})(1 - s_\mathrm{i}))$. Further, the focal group may attack one other group. With probability $1 - a$, this does not happen, and in this case the focal sex-i young adult does not have the opportunity to obtain additional breeding spots. Alternatively, the focal group attacks the other group with probability a and loses the war with probability $1 - \omega'$, where $\omega' = \omega(\Omega_\mathrm{m}', \Omega_\mathrm{f}', \bar{\Omega}_\mathrm{m}, \bar{\Omega}_\mathrm{f})$, which again results in no additional opportunities for breeding spots. Otherwise, the focal group wins with probability ω' and in this case the focal sex-i young adult has access to an additional $N_\mathrm{i}(1 - s_\mathrm{i})$ breeding spots, for which he competes with $N_\mathrm{f}K_\mathrm{i}(1 - s_\mathrm{i})$ sex-i young adults from their group and $N_\mathrm{f}K_\mathrm{i}s_\mathrm{i}$ sex-i young adults from the conquered group. Thus, adding the appropriate competitiveness modifiers, the focal sex-i young adult obtains a breeding spot in the defeated group with probability $N_\mathrm{i}\tau_\mathrm{i}(\Omega_\mathrm{i})(1 - s_\mathrm{i})/(N_\mathrm{f}K_\mathrm{i}\tau_\mathrm{i}(\Omega_\mathrm{i}')(1 - s_\mathrm{i})+ N_\mathrm{f}K_\mathrm{i}\tau_\mathrm{i}(\bar{\Omega}_\mathrm{i})s_\mathrm{i})$. Alternatively, the focal sex-i young adult migrates from the natal group with probability m_i to a randomly chosen group. In this case, fitness is identical to the philopatry case and the migration terms cancel out (N.B. migration rates influence the relatedness structure of the population, see CONSANGUINITY AND RELATEDNESS). Therefore, the absolute fitness of a focal sex-i young adult is equal to:

$$w_\mathrm{i} = \left((1-a) + a\left((1-\omega'')\frac{\tau_\mathrm{i}(\Omega_\mathrm{i})}{\tau_\mathrm{i}(\Omega_\mathrm{i}')} + \omega''\frac{\tau_\mathrm{i}(\Omega_\mathrm{i})s_\mathrm{i}}{\tau_\mathrm{i}(\Omega_\mathrm{i}')s_\mathrm{i} + \tau_\mathrm{i}(\bar{\Omega}_\mathrm{i})(1-s_\mathrm{i})}\right) + a\,\omega'\frac{\tau_\mathrm{i}(\Omega_\mathrm{i})(1-s_\mathrm{i})}{\tau_\mathrm{i}(\Omega_\mathrm{i}')(1-s_\mathrm{i}) + \tau_\mathrm{i}(\bar{\Omega}_\mathrm{i})s_\mathrm{i}}\right)\frac{N_\mathrm{i}}{N_\mathrm{f}K_\mathrm{i}} \qquad \text{[A3.1]}$$

The average fitness of a sex-i young adult in the population is $\bar{w}_\mathrm{i} = N_\mathrm{i}/(N_\mathrm{f}K_\mathrm{i})$ and the relative fitness of the focal sex-i young adult is given by $W_\mathrm{i} = w_\mathrm{i} / \bar{w}_\mathrm{i}$.

Participation

MARGINAL FITNESS

In a sex-structured population, the relative fitness of an individual of unspecified sex is given by $W = c_m W_m + c_f W_f$ which is an average of the fitness of the two sexes, weighted by the class reproductive values of the two sexes, c_m and c_f (Fisher, 1930; Price and Smith, 1972; Taylor and Frank, 1996; Frank, 1997; Taylor, et al., 2007). Consider a locus $\mathcal{G}$, which controls participation of sex i ∈{m,f} Ω_i, a trait expressed only by young adults of sex i. Let g be the genic value of the focal individual for this gene, G the breeding value of the focal individual, G' the breeding value of a randomly-chosen groupmate of the focal individual, and $\bar{G}$ the average of the population. Under the assumption of vanishing genetic variation – all breeding values of the population clustered around the mean (Taylor and Frank 1996; Frank 1997) – the direction of natural selection is given by:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_\mathrm{m}\frac{\mathrm{d}W_\mathrm{m}}{\mathrm{d}g_\mathrm{m}} + c_\mathrm{f}\frac{\mathrm{d}W_\mathrm{f}}{\mathrm{d}g_\mathrm{f}}, \qquad [A3.2]$$

with all derivatives evaluated at $g = g_m = g_f = \bar{G}$.

The derivative $\mathrm{d}W_i/\mathrm{d}g_i$ describes the impact of the genic value of a gene drawn from a young adult of sex i on their relative fitness. It can be expanded to reveal a direct fitness component (first addend), an indirect fitness component (second addend) and associations between genic values, breeding values and phenotypes (derivatives), obtaining:

$$\frac{\mathrm{d}W_\mathrm{i}}{\mathrm{d}g_\mathrm{i}} = \frac{\partial W_\mathrm{i}}{\partial \Omega_\mathrm{i}}\frac{\mathrm{d}\Omega_\mathrm{i}}{\mathrm{d}G}\frac{\mathrm{d}G}{\mathrm{d}g_\mathrm{i}} + \frac{\partial W_\mathrm{i}}{\partial \Omega_\mathrm{i}'}\frac{\mathrm{d}\Omega_\mathrm{i}'}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_\mathrm{i}} = \left(\frac{\partial W_\mathrm{i}}{\partial \Omega_\mathrm{i}}p_\mathrm{self} + \frac{\partial W_\mathrm{i}}{\partial \Omega_\mathrm{i}'}p_\mathrm{ii}\right)\gamma\,, \qquad [A3.3]$$

where $\mathrm{d}W_i/\mathrm{d}\Omega_i$ is the impact of the participation phenotype of the focal sex-i individual on their fitness, $\mathrm{d}W_i/\mathrm{d}\Omega_i'$ is the impact of the participation phenotype of a random sex-i individual on the fitness of the focal sex-i individual, $p_{self} = \mathrm{d}G/\mathrm{d}g_i$ is the consanguinity of the focal individual of sex i to themselves, $p_{ii} = \mathrm{d}G'/\mathrm{d}g_i$ is the consanguinity between the focal individual of sex i and a random individual of the same sex in their group, and $\gamma =$

$d\Omega_i/dG = d\Omega_i'/dG'$ is the correlation between an individual's phenotype and their breeding value.

Analogously, the derivative dW_j/dg_j describes the impact of the genic value of a gene drawn from a young adult of the other sex on their relative fitness. It can be expanded to reveal the indirect fitness component (there is no direct fitness component, as the phenotype is expressed by young adults of sex i alone) and associations between genic values, breeding values and phenotypes (derivatives), obtaining:

$$\frac{dW_j}{dg_j} = \frac{\partial W_j}{\partial \Omega_i{}'} \frac{d\Omega_i{}'}{dG'} \frac{dG'}{dg_j} = \frac{\partial W_j}{\partial \Omega_i{}'} \, p_{ij} \, \gamma \,, \qquad \text{[A3.4]}$$

where $dW_j/d\Omega_i'$ is the impact of the participation phenotype of a random sex-i individual on the fitness of the focal individual of the other sex, $p_{ij} = dG'/dg_j$ is the consanguinity between the focal individual of the other sex and a random sex-i individual in their group, and $\gamma = d\Omega_i'/dG'$ is the correlation between an individual's phenotype and their breeding value.

Both ω and τ_i are functions of Ω_i (see Methods). Therefore: $\partial W_i/\partial\Omega_i = (\partial W_i/\partial\tau_i(\Omega_i))(\partial\tau_i(\Omega_i)/\partial\Omega_i)$, $\partial W_i/\partial\Omega_i' = (\partial W_i/\partial\omega')(\partial\omega'/\partial\Omega_i') - (\partial W_i/\partial\omega'')(\partial\omega''/\partial\Omega_i') + (\partial W_i/\partial\tau_i(\Omega_i'))(\partial\tau_i(\Omega_i')/\partial\Omega_i')$, and $\partial W_j/\partial\Omega_i' = (\partial W_j/\partial\omega')(\partial \omega'/\partial\Omega_i') - (\partial W_j/\partial\omega'')(\partial\omega''/\partial\Omega_i')$, where $\partial\tau_i(\Omega_i)/\partial\Omega_i = \partial\tau_i(\Omega_i')/\partial\Omega_i' = -\tau_i(\bar{\Omega}_i)\, c_i$ and $\partial\omega'/\partial\Omega_i' = -\partial\omega''/\partial\Omega_i' = b_i$. Substituting these expressions and Eq. A3.3-A3.4 into Eq. A3.2, we obtain:

$$\frac{dW}{dg} = c_i \left(\frac{\partial W_i}{\partial\tau_i(\Omega_i)} \left(-\tau_i(\bar{\Omega}_i) c_i\right) p_{self} + \left(\frac{\partial W_i}{\partial\omega'} \, b_i + \frac{\partial W_i}{\partial\omega''} \, b_i + \frac{\partial W_i}{\partial\tau_i(\Omega_i{}')} \left(-\tau_i(\bar{\Omega}_i) c_i\right) \right) p_{ii} \right) \gamma \; + c_j \left(\frac{\partial W_j}{\partial\omega'} \, b_i + \frac{\partial W_j}{\partial\omega''} b_i \right) p_{ij} \, \gamma \qquad \text{[A3.5]}$$

Population average participation of sex i increases whenever the condition $dW/dg > 0$ is respected. Considering that $c_f = c_m = 1/2$ under diploid inheritance, this condition is given by:

$$-c_i p_{self} + \left(1 - 2\,\bar{\omega}\, s_i \,(1 - s_i)\right) c_i p_{ii} + 2(1 - s_i) b_i p_{ii} + 2\left(1 - s_j\right) b_i p_{ij} > 0 \qquad \text{[A3.6]}$$

Dividing by p_{self} to obtain $r_{ii} = p_{ii}/p_{self}$ and $r_{ij} = p_{ij}/p_{self}$ (see CONSANGUINITY AND RELATEDNESS) and rearranging terms yields condition [3.1] in Results.

CONSANGUINITY AND RELATEDNESS

Given two individuals, A and B, and a locus, the coefficient of consanguinity between the two at that locus, p_{AB}, is equal to the probability of identity-by-descent between a gene randomly-drawn from that locus in individual A and a gene randomly-drawn from the same locus in individual B (Bulmer, 1994). In the case in which the second individual coincides with the first, i.e. B=A, the consanguinity of an individual to themselves is obtained and it is given by $p_{\mathrm{self}} = (1 + f)/2$. The inbreeding coefficient f is the consanguinity between two mating partners, one from each sex, in a post-competition group and it is given by $f = \varphi_{\mathrm{mf}}\, p_{\mathrm{x}}$. Analogously, the consanguinity of two sex-i adults in a post-competition group is given by $p_{\mathrm{ii,adult}} = \varphi_{\mathrm{ii}}\, p_{\mathrm{x}}$, where again $\mathrm{i} \in \{\mathrm{m,f}\}$. The coefficients $\varphi_{\mathrm{mf}} = (1 - \bar{a}\,\bar{\omega}\,(2s_{\mathrm{m}}s_{\mathrm{f}} - s_{\mathrm{m}} - s_{\mathrm{f}})(1 - m_{\mathrm{m}})(1 - m_{\mathrm{f}})$ and $\varphi_{\mathrm{ii}} = (1 - 2\,\bar{a}\,\bar{\omega}\,s_{\mathrm{i}}(1 - s_{\mathrm{i}}))(1 - m_{\mathrm{i}})^2$ are the probabilities that two adults of opposite sex and two sex-i adults, respectively, who are in the same post-competition group, were born in the same group. p_{x} is the consanguinity of individuals born in the same group and is given by:

$$p_{\mathrm{x}} = \frac{1}{4}\left(\frac{1}{N_{\mathrm{m}}} p_{\mathrm{self}} + \frac{N_{\mathrm{m}}-1}{N_{\mathrm{m}}} p_{\mathrm{mm,adult}}\right) + \frac{1}{2} f + \frac{1}{4}\left(\frac{1}{N_{\mathrm{f}}} p_{\mathrm{self}} + \frac{N_{\mathrm{f}}-1}{N_{\mathrm{f}}} p_{\mathrm{ff,adult}}\right) \qquad [\mathrm{A3.7}]$$

which, substituting the appropriate consanguinities and solving for p_{x}, becomes:

$$p_{\mathrm{x}} = \frac{(N_{\mathrm{m}}+N_{\mathrm{f}})\,\varphi_{\mathrm{mf}}}{8\,N_{\mathrm{m}}\,N_{\mathrm{f}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{mm}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{ff}} - (4N_{\mathrm{m}}\,N_{\mathrm{f}} + N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{mf}}}. \qquad [\mathrm{A3.8}]$$

The consanguinity of a focal sex-i young adult to a random young adult of the same sex in their post-migration group is equal to the probability that they were born in the same group and that neither migrated, namely $p_{\mathrm{ii}} = (1 - m_{\mathrm{i}})^2\, p_{\mathrm{x}}$. Analogously, the consanguinity of the focal sex-i young adult to a random young adult of the opposite sex in their post-migration group is given by $p_{\mathrm{ij}} = (1 - m_{\mathrm{i}})(1 - m_{\mathrm{j}})\, p_{\mathrm{x}}$.

Given again two individuals, A and B, the coefficient of relatedness between the two, r_{AB}, is equal to the consanguinity of individual B to individual A, p_{AB}, divided by the consanguinity of individual B to themselves, $p_{\mathrm{BB}} = p_{\mathrm{self}}$ (Bulmer, 1994). Therefore, the relatedness of individuals born in the same group is given by $r_x = p_x/p_{self}$, the relatedness of a focal sex-i young adult to a random young adult of the same sex in their post-migration group is given by $r_{ii} = p_{ii}/p_{self} = (1 - m_i)^2\, r_x$ and the relatedness of a focal sex-i young adult to a random young adult of the other sex in their post-migration group is given by $r_{ij} = p_{ij}/p_{self} = (1 - m_i)(1 - m_j)\, r_x$.

Participation equilibria in the absence of other sex differences in the ecology of war

Consider a case in which there are no sex differences in the ecology of war other than potential differences in participation: $b_i(\Omega_i, \Omega_j) = b(\Omega_i, \Omega_j) = b(\Omega_j, \Omega_i)$, $c_i(\Omega_i) = c(\Omega_i)$, $m_i = m$, and $s_i = s$, for all $i \in \{m,f\}$. It follows that $r_{ii} = r_{ij} = r$ and $s_i(1\text{-}s_i) = M_i = M$ (admixture). Therefore, the marginal fitness function for the participation of sex i is given by $\theta_i = 4(1 - s)rb(\bar{\Omega}_i, \bar{\Omega}_j) - (1 - (1 - 2\varpi M)r)c(\bar{\Omega}_i)$. Notice that the two marginal fitness functions for the two sexes are completely symmetrical. That is, one can be obtained from the other simply by exchanging i and j labels. This implies that, in a streamline plot (see Fig. 3.1), streamlines and equilibria for the participation of the two sexes are symmetrical with respect to the (0,0)-(1,1) diagonal, independently of the specific functional forms of *c* and *b*.

We now derive the condition for pairs of participation values of the two sexes to be equilibria and for these equilibria to be stable. For simplicity, we make three assumptions:

Assumption 1: The benefit function *b* is a strictly monotonically increasing or decreasing function of the participation of sex i. This can be expressed mathematically as:

$$\left(\frac{\partial b(\bar{\Omega}_i,\bar{\Omega}_j)}{\partial \bar{\Omega}_i}\Big|_{\bar{\Omega}_i=\hat{\Omega},\, \bar{\Omega}_j=\hat{\Omega}'} < 0\right) \vee \left(\frac{\partial b(\bar{\Omega}_i,\bar{\Omega}_j)}{\partial \bar{\Omega}_i}\Big|_{\bar{\Omega}_i=\hat{\Omega},\, \bar{\Omega}_j=\hat{\Omega}'} > 0\right) \forall \hat{\Omega}, \hat{\Omega}' \in [0,1]. \qquad [A3.9]$$

Assumption 2: The cost function *c* is a strictly monotonically increasing or decreasing function of the participation of sex i. This can be expressed mathematically as:

$$\left(\frac{\partial c(\bar{\Omega}_{\mathrm{i}})}{\partial \bar{\Omega}_{\mathrm{i}}}\Big|_{\bar{\Omega}_i=\hat{\Omega}} < 0\right) \vee \left(\frac{\partial c(\bar{\Omega}_{\mathrm{i}})}{\partial \bar{\Omega}_{\mathrm{i}}}\Big|_{\bar{\Omega}_i=\hat{\Omega}} > 0\right) \forall \hat{\Omega} \in [0,1]. \qquad \text{[A3.10]}$$

Assumption 3: The ratio of the benefit function and the cost function is a strictly monotonically increasing or decreasing function of the participation of sex i. This can be expressed mathematically as:

$$\left(\frac{\partial\left(\frac{b\left(\bar{\Omega}_{\mathrm{i}},\bar{\Omega}_{\mathrm{j}}\right)}{c(\bar{\Omega}_{\mathrm{i}})}\right)}{\partial \bar{\Omega}_{\mathrm{i}}}\Big|_{\bar{\Omega}_i=\hat{\Omega},\, \bar{\Omega}_j=\hat{\Omega}'} < 0\right) \vee \left(\frac{\partial\left(\frac{b\left(\bar{\Omega}_{\mathrm{i}},\bar{\Omega}_{\mathrm{j}}\right)}{c(\bar{\Omega}_{\mathrm{i}})}\right)}{\partial \bar{\Omega}_{\mathrm{i}}}\Big|_{\bar{\Omega}_i=\hat{\Omega},\, \bar{\Omega}_j=\hat{\Omega}'} > 0\right) \forall \hat{\Omega}, \hat{\Omega}' \in [0,1]. \qquad \text{[A3.11]}$$

Considering that each participation term can assume either boundary (0 and 1) or intermediate values, we need to consider ten separate cases: the four corners of the square, the four sides, the diagonal, and the interior (non-diagonal).

i) $\bar{\Omega}_{\mathrm{i}} = 0$, for all i ∈{m,f}; The condition for this point to be a stable equilibrium is that the marginal fitness for participation of the two sexes are both negative, i.e. $\theta_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=0,\bar{\Omega}_{\mathrm{j}}=0} < 0$. If c(0)>0, this requires $b(0,0)/c(0) < P$, where $P = (1-(1-2\varpi M)r)/4(1-s)r$. If c(0)<0, this requires $b(0,0)/c(0) > P$, which can never be satisfied.

ii) $\bar{\Omega}_{\mathrm{i}} = 1$, for all i ∈{m,f}; The condition for this point to be a stable equilibrium is that the marginal fitness for participation of the two sexes are both positive, i.e. $\theta_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=1,\bar{\Omega}_{\mathrm{j}}=1} > 0$. If c(0)>0, this requires $b(1,1)/c(1) > P$. If c(0)<0, it requires $b(1,1)/c(1) < P$.

iii) $\bar{\Omega}_i = 1$ and $\bar{\Omega}_j = 0$, for all i ∈{m,f} and j ∈{m,f}, j≠i; The condition for this point to be a stable equilibrium is that the marginal fitness for participation of sex i is positive and that of the other sex is negative, i.e. $\theta_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=1,\bar{\Omega}_{\mathrm{j}}=0} > 0$ and $\theta_{\mathrm{j}}|_{\bar{\Omega}_{\mathrm{j}}=0,\bar{\Omega}_{\mathrm{i}}=1} < 0$. We consider the four possible cases:

1) If $c(0)>0$ and $c(1)>0$, the condition requires $b(0,1)/c(0) < P < b(1,0)/c(1)$, and considering Assumption 2, this implies $\partial c(\bar{\Omega}_\mathrm{i})/\partial\bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i}=\hat{\Omega}} < 0 \ \forall\hat{\Omega} \in [0,1]$.

2) If $c(0)<0$ and $c(1)>0$, the condition requires $b(0,1)/c(0) > P$ and $b(1,0)/c(1) > P$, and the former is never satisfied.

3) If $c(0)>0$ and $c(1)<0$, the condition requires $b(1,0)/c(1) < b(0,1)/c(0) < P$, and considering Assumption 2, this implies $\partial c(\bar{\Omega}_\mathrm{i})/\partial\bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i}=\hat{\Omega}} < 0 \ \forall\hat{\Omega} \in [0,1]$.

4) If $c(0)<0$ and $c(1)<0$, the condition requires $b(0,1)/c(0) > P$ and $b(1,0)/c(1) < P$, and the former is never satisfied.

iv) $\bar{\Omega}_i = 0$ and $\bar{\Omega}_j = 1$, for all i $\in$ {m,f} and j $\in$ {m,f}, j≠i; the condition for this point to be a stable equilibrium is identical to that of case iii). Therefore, when (1,0) is stable, (0,1) is also stable, and vice versa.

v) $\bar{\Omega}_\mathrm{i} = \tilde{\Omega} \neq 0,1$ and $\bar{\Omega}_\mathrm{j} = 0$, for all i $\in$ {m,f} and j $\in$ {m,f}, j≠i; The condition for this point to be an equilibrium is that the marginal fitness for participation of sex i is equal to zero and that of the other sex is negative, i.e. $\theta_\mathrm{i}|_{\bar{\Omega}_\mathrm{i}=\tilde{\Omega}\neq 0,1,\,\bar{\Omega}_\mathrm{j}=0} = 0$ and $\theta_\mathrm{j}|_{\bar{\Omega}_\mathrm{j}=0,\,\bar{\Omega}_\mathrm{i}=\tilde{\Omega}\neq 0,1} < 0$. We consider the four possible cases:

1) If $c(\tilde{\Omega}) > 0$ and $c(0)>0$, the condition requires $b(0,\tilde{\Omega})/c(0) < b(\tilde{\Omega},0)/c(\tilde{\Omega}) = P$. Considering Assumption 2, this implies $\partial c(\bar{\Omega}_\mathrm{i})/\partial\bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i}=\hat{\Omega}} < 0 \ \forall\hat{\Omega} \in [0,1]$. If an equilibrium exists, the condition for it to be stable is that $\partial\theta_\mathrm{i}/\partial\bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i}=\tilde{\Omega}\neq 0,1,\,\bar{\Omega}_\mathrm{j}=0} < 0$, which requires $\partial b(\bar{\Omega}_\mathrm{i},\bar{\Omega}_\mathrm{j})/\partial\bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i}=\tilde{\Omega}\neq 0,1,\,\bar{\Omega}_\mathrm{j}=0} < P\partial b(\bar{\Omega}_\mathrm{i})/\partial\bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i}=\tilde{\Omega}\neq 0,1,\,\bar{\Omega}_\mathrm{j}=0}$. Considering Assumption 1, this implies $\left(\partial b(\bar{\Omega}_i,\bar{\Omega}_j)/\partial\bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_i=\hat{\Omega},\,\bar{\Omega}_j=\hat{\Omega}'} < 0\right) \forall\hat{\Omega},\hat{\Omega}' \in [0,1]$.

2) If $c(\tilde{\Omega}) > 0$ and $c(0)<0$, the condition requires $b(\tilde{\Omega},0)/c(\tilde{\Omega}) = P$ and $b(0,\tilde{\Omega})/c(0) > P$, and the latter can never be satisfied.

3) If $c(\tilde{\Omega}) < 0$ and $c(0)>0$, the condition requires $b(\tilde{\Omega},0)/c(\tilde{\Omega}) = P$ and $b(0,\tilde{\Omega})/c(0) < P$, and the former can never be satisfied.

4)If $c(\tilde{\Omega}) < 0$ and $c(0)<0$, the condition requires $b(\tilde{\Omega}, 0)/c(\tilde{\Omega}) = P$ and $b(0, \tilde{\Omega})/c(0) > P$, and neither can be satisfied.

vi) $\bar{\Omega}_{\mathrm{i}} = 0$ and $\bar{\Omega}_{\mathrm{j}} = \tilde{\Omega} \neq 0,1$, for all i ∈{m,f} and j ∈{m,f}, j≠i; the condition for this point to be a stable equilibrium is identical to that of case v). Therefore, when$(\tilde{\Omega}, 0)$ is stable, $(0, \tilde{\Omega})$ is also stable, and vice versa.

vii) $\bar{\Omega}_{\mathrm{i}} = 1$ and $\bar{\Omega}_{\mathrm{j}} = \tilde{\Omega} \neq 0,1,$ for all $\mathrm{i} \in \{\mathrm{m},\mathrm{f}\}$ and $\mathrm{j} \in \{\mathrm{m},\mathrm{f}\}, \mathrm{j} \neq \mathrm{i}$; the condition for this point to be an equilibrium is that the marginal fitness for participation of sex i is positive and that of the other sex is equal to zero, i.e. $\theta_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=1, \bar{\Omega}_{\mathrm{j}}=\tilde{\Omega}\neq 0,1} > 0$ and $\theta_{\mathrm{j}}|_{\bar{\Omega}_{\mathrm{j}}=\tilde{\Omega}\neq 0,1, \bar{\Omega}_{\mathrm{i}}=1} = 0$. We consider the four possible cases:

1) If $c(\tilde{\Omega}) > 0$ and $c(1)>0$, the condition requires $b(1, \tilde{\Omega})/c(1) > b(\tilde{\Omega}, 1)/c(\tilde{\Omega}) = P$. Considering Assumption 2, this implies $\partial c(\bar{\Omega}_{\mathrm{i}})/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=\hat{\Omega}} < 0 \; \forall \hat{\Omega} \in [0,1]$. If an equilibrium exists, the condition for it to be stable is that $\partial \theta_{\mathrm{i}}/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=1, \bar{\Omega}_{\mathrm{j}}=\tilde{\Omega}\neq 0,1} < 0$, which requires $\partial b(\bar{\Omega}_{\mathrm{i}}, \bar{\Omega}_{\mathrm{j}})/\partial \bar{\Omega}_{\mathrm{j}}|_{\bar{\Omega}_{\mathrm{i}}=1, \bar{\Omega}_{\mathrm{j}}=\tilde{\Omega}\neq 0,1} < P\partial b(\bar{\Omega}_{\mathrm{j}})/\partial \bar{\Omega}_{\mathrm{j}}|_{\bar{\Omega}_{\mathrm{i}}=1, \bar{\Omega}_{\mathrm{j}}=\tilde{\Omega}\neq 0,1}$. Considering Assumption 1, this implies $\left(\partial b(\bar{\Omega}_i, \bar{\Omega}_j)/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_i=\hat{\Omega}, \bar{\Omega}_j=\hat{\Omega}'} < 0\right) \forall \hat{\Omega}, \hat{\Omega}' \in [0,1]$.

2) If $c(\tilde{\Omega}) > 0$ and $c(1)<0$, the condition which requires $b(1, \tilde{\Omega})/c(1) < b(\tilde{\Omega}, 1)/c(\tilde{\Omega}) = P$. Considering Assumption 2, this implies $\partial c(\bar{\Omega}_{\mathrm{i}})/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=\hat{\Omega}} < 0 \; \forall \hat{\Omega} \in [0,1]$. If an equilibrium exists, the condition for it to be stable is that $\partial \theta_{\mathrm{i}}/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=1, \bar{\Omega}_{\mathrm{j}}=\tilde{\Omega}\neq 0,1} < 0$, which requires $\partial b(\bar{\Omega}_{\mathrm{i}}, \bar{\Omega}_{\mathrm{j}})/\partial \bar{\Omega}_{\mathrm{j}}|_{\bar{\Omega}_{\mathrm{i}}=1, \bar{\Omega}_{\mathrm{j}}=\tilde{\Omega}\neq 0,1} < P\partial b(\bar{\Omega}_{\mathrm{j}})/\partial \bar{\Omega}_{\mathrm{j}}|_{\bar{\Omega}_{\mathrm{i}}=1, \bar{\Omega}_{\mathrm{j}}=\tilde{\Omega}\neq 0,1}$. Considering Assumption 1, this implies $\left(\partial b(\bar{\Omega}_i, \bar{\Omega}_j)/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_i=\hat{\Omega}, \bar{\Omega}_j=\hat{\Omega}'} < 0\right) \forall \hat{\Omega}, \hat{\Omega}' \in [0,1]$.

3) If $c(\tilde{\Omega}) < 0$ and $c(1)>0$, the condition requires $b(\tilde{\Omega}, 1)/c(\tilde{\Omega}) = P$ and $b(1, \tilde{\Omega})/c(1) > P$, and the former can never be satisfied.

4)If $c\big(\tilde{\Omega}\big) < 0$ and $c(1)<0$, the condition requires $b(\tilde{\Omega}, 1)/c(\tilde{\Omega}) = P$ and $\frac{b(1,\tilde{\Omega})}{c(1)} < P$, and the former can never be satisfied.

viii) $\bar{\Omega}_\mathrm{i} = \tilde{\Omega} \neq 0{,}1$ and $\bar{\Omega}_\mathrm{j} = 1$, for all i ∈{m,f} and j ∈{m,f}, j≠i; the condition for this point to be a stable equilibrium is identical to that of case vii). Therefore, when$(\tilde{\Omega}, 1)$ is stable, $(1, \tilde{\Omega})$ is also stable, and vice versa.

ix) $\bar{\Omega}_\mathrm{i} = \tilde{\Omega} \neq 0{,}1$, for all i∈ {m,f}; The condition for a point on the diagonal to be an equilibrium is that the marginal fitness for participation of sex i is equal to that of the other sex and both are equal to zero, i.e. $\theta_\mathrm{i}|_{\bar{\Omega}_\mathrm{i} = \tilde{\Omega} \neq 0,1} = 0$, which requires $b(\bar{\Omega}_\mathrm{i}, \bar{\Omega}_\mathrm{j})/c(\bar{\Omega}_\mathrm{i})|_{\bar{\Omega}_\mathrm{i} = \tilde{\Omega} \neq 0,1} = P$. This condition can only be satisfied if $c(\bar{\Omega}_\mathrm{i})|_{\bar{\Omega}_\mathrm{i} = \tilde{\Omega} \neq 0,1} > 0$. Considering Assumption 3, there cannot be more than one equilibrium on the diagonal. If an equilibrium exists, the condition for it to be stable is that both eigenvalues of the Jacobian matrix of the model are negative. The Jacobian matrix of the model is:

$$J = \begin{pmatrix} \frac{\partial \theta_\mathrm{i}}{\partial \bar{\Omega}_\mathrm{i}} & \frac{\partial \theta_\mathrm{i}}{\partial \bar{\Omega}_\mathrm{j}} \\ \frac{\partial \theta_\mathrm{i}}{\partial \bar{\Omega}_\mathrm{j}} & \frac{\partial \theta_\mathrm{i}}{\partial \bar{\Omega}_\mathrm{i}} \end{pmatrix} \tag{A3.12}$$

The condition for both eigenvalues of the matrix to be negative is $\partial c(\bar{\Omega}_\mathrm{i})/\partial \bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i} = \hat{\Omega}} > 0 \ \forall \hat{\Omega} \in [0{,}1]$ and $\partial b(\bar{\Omega}_\mathrm{i}, \bar{\Omega}_\mathrm{j})/\partial \bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i} = \tilde{\Omega} \neq 0,1} = ½ P \partial c(\bar{\Omega}_\mathrm{i})/\partial \bar{\Omega}_\mathrm{i}|_{\bar{\Omega}_\mathrm{i} = \tilde{\Omega} \neq 0,1}$.

x) $\bar{\Omega}_\mathrm{i} \neq \bar{\Omega}_\mathrm{j} \neq 0{,}1$, for all i ∈{m,f} and j ∈{m,f}, j≠i; the marginal fitness functions for participation of the two sexes are identical with the exception of $c(\bar{\Omega}_\mathrm{i}) = c(\bar{\Omega}_\mathrm{j})$. The condition for this point to be a stable equilibrium is that $\theta_\mathrm{i}|_{\bar{\Omega}_\mathrm{i} \neq \bar{\Omega}_\mathrm{j} \neq 0,1} = \theta_\mathrm{j}|_{\bar{\Omega}_\mathrm{i} \neq \bar{\Omega}_\mathrm{j} \neq 0,1} = 0$, which requires $b(\bar{\Omega}_\mathrm{i}, \bar{\Omega}_\mathrm{j})/c(\bar{\Omega}_\mathrm{i})|_{\bar{\Omega}_\mathrm{i} \neq \bar{\Omega}_\mathrm{j} \neq 0,1} = b(\bar{\Omega}_\mathrm{j}, \bar{\Omega}_\mathrm{i})/c(\bar{\Omega}_\mathrm{j})|_{\bar{\Omega}_\mathrm{i} \neq \bar{\Omega}_\mathrm{j} \neq 0,1} = P$. Since $\bar{\Omega}_\mathrm{i} \neq \bar{\Omega}_\mathrm{j}$, this is impossible. Points $(\bar{\Omega}_\mathrm{i}, \bar{\Omega}_\mathrm{j})$ with $\bar{\Omega}_\mathrm{i} \neq \bar{\Omega}_\mathrm{j} \neq 0{,}1$ can never be equilibria.

We now seek to demonstrate that nine equilibria configurations are not allowed. We consider them in turn:

I) stable equilibria at $(\tilde{\Omega}, 0)$ with $\tilde{\Omega} \neq 0{,}1$ and $(1{,}0)$; this requires $b(\tilde{\Omega}, 0)/c(\tilde{\Omega}) < b(1{,}0)/c(1)$. Since costs are required to be decelerating, it follows that $c\big(\tilde{\Omega}\big) > c(1)$. As a consequence, $b(1{,}0) > b(\tilde{\Omega}, 0)$, but this is impossible because benefits are required to be decelerating. This stable equilibria configuration is thus not allowed.

II) stable equilibria at $(0, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$ and $(0{,}1)$; this case is analogous to case I) above.

III) stable equilibria at $(1, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$ and $(1{,}0)$ this requires $b(\tilde{\Omega}, 1)/b(1{,}0) < c(\tilde{\Omega})/c(1)$. Since costs are required to be decelerating, it follows that $c\big(\tilde{\Omega}\big) > c(1)$. As a consequence, $b(1{,}0) > b(\tilde{\Omega}, 0)$, but this is impossible because benefits are required to be decelerating. This stable equilibria configuration is thus not allowed.

IV) stable equilibria at $(\tilde{\Omega}, 1)$ with $\tilde{\Omega} \neq 0{,}1$ and $(0{,}1)$; this case is analogous to case III) above.

V) stable equilibria at $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$ and $(0, 0)$; this requires $b(0{,}0)/c(0) < b(1{,}1)/c(1)$, which itself requires $\partial(b(\bar{\Omega}_{\mathrm{i}}, \bar{\Omega}_{\mathrm{j}})/c(\bar{\Omega}_{\mathrm{i}}))/\partial\bar{\Omega}_{\mathrm{i}} > 0$ and as a consequence $(\partial b(\bar{\Omega}_{\mathrm{i}}, \bar{\Omega}_{\mathrm{j}})/\partial\bar{\Omega}_{\mathrm{i}})c(\bar{\Omega}_{\mathrm{i}}) - b(\bar{\Omega}_{\mathrm{i}}, \bar{\Omega}_{\mathrm{j}})(\partial c(\bar{\Omega}_{\mathrm{i}})/\partial\bar{\Omega}_{\mathrm{i}}) > 0$ which contradicts part of the condition for the first point to be an equilibrium (i.e. $\partial b(\bar{\Omega}_{\mathrm{i}}, \bar{\Omega}_{\mathrm{j}})/\partial\bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=\tilde{\Omega}\neq 0,1} = ½P\partial c(\bar{\Omega}_{\mathrm{i}})/\partial\bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=\tilde{\Omega}\neq 0,1}$, see case ix) above).

VI) stable equilibria at $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$ and $(0, 0)$; this case is analogous to case V) above.

VII) stable equilibria at $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$ and $(1, 0)$ (or $(1, 0)$); the first point requires accelerating costs, while the second one requires decelerating costs. This stable equilibria configuration is thus not allowed.

VIII) stable equilibria at $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$ $(0, \tilde{\Omega}')$ with $\tilde{\Omega}' \neq 0{,}1$ (or $(\tilde{\Omega}', 0)$); the first point requires accelerating costs, while the second one requires decelerating costs. This stable equilibria configuration is thus not allowed.

IX) stable equilibria at $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$ $(1, \tilde{\Omega}')$ with $\tilde{\Omega}' \neq 0{,}1$ (or $(\tilde{\Omega}', 1)$); the first point requires accelerating costs, while the second one requires decelerating costs. This stable equilibria configuration is thus not allowed.

Therefore, for any given set of parameters, two classes of stable equilibria configurations may be obtained depending on the cost function:

a) If costs are accelerating $(\partial c(\bar{\Omega}_{\mathrm{i}})/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=\hat{\Omega}} > 0 \ \forall \hat{\Omega} \in [0{,}1])$, there is always at least one stable equilibrium, either: a.1) one and only one stable equilibrium on the diagonal $(\tilde{\Omega}, \tilde{\Omega})$, extremes included; or a.2) a stable equilibrium on (0,0) and one on (1,1).

b) If costs are decelerating $(\partial c(\bar{\Omega}_{\mathrm{i}})/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=\hat{\Omega}} > 0 \ \forall \hat{\Omega} \in [0{,}1])$, there is always at least one stable equilibrium, which cannot be on the diagonal. All equilibria configurations not excluded in cases I-IX) above are allowed and therefore possible configurations are: b.1) (0,0) and (1,1); b.2) (0,0); b.3) (1,1); b.4) $(0, \tilde{\Omega})$ and $(\tilde{\Omega}, 0)$; b.5) $(1, \tilde{\Omega})$ and $(\tilde{\Omega}, 1)$; b.6) $(0, \tilde{\Omega})$, $(\tilde{\Omega}, 0)$, $(1, \tilde{\Omega}')$ and $(\tilde{\Omega}', 1)$; b.7) (0,1) and (1,0); b.8) (0,1), (1,0), (0,0); b.9) (0,1), (1,0), (1,1).

FEEDBACKS BETWEEN MALE AND FEMALE PARTICIPATION

The impact of increased participation of young adults (hereafter, "individuals") of sex i $\in\{m,f\}$ on participation of individuals of the same sex is given by:

$$\frac{\partial \theta_{\mathrm{i}}}{\partial \bar{\Omega}_{\mathrm{i}}} = 4(1-s)r\frac{\partial b_{\mathrm{i}}}{\partial \bar{\Omega}_{\mathrm{i}}} - \big(1-\big(1-2\bar{\omega}s(1-s)\big)r\big)\frac{\partial c_{\mathrm{i}}}{\partial \bar{\Omega}_{\mathrm{i}}}, \qquad \text{[A3.13]}$$

which is equal to the l.h.s. of condition [3.2] in Results. Analogously, the impact of increased participation of individuals of sex i on participation of individuals of the other sex is given by:

$$\frac{\partial \theta_{\mathrm{j}}}{\partial \bar{\Omega}_{\mathrm{i}}} = 4(1-s)r\frac{\partial b_{\mathrm{j}}}{\partial \bar{\Omega}_{\mathrm{i}}}, \qquad \text{[A3.14]}$$

which is equal to the l.h.s. of condition [3.3] in Results.

Whether personal costs for individuals of one sex increase with increasing participation of that same sex (“accelerating costs”) or decrease with increasing participation of that same sex (“decelerating costs”), determines the nature of the feedbacks between male and female participation. Personal costs of warfare consist in a loss of competitive ability for breeding spots. Competition for reproduction is fundamentally within-sex, because the total reproductive value of each sex is fixed (and, indeed, in this non-overlapping generations scenario, they are both equal to one half (Fisher, 1930; Grafen, 2014)).

If costs are accelerating ($\partial c(\bar{\Omega}_{\mathrm{i}})/\partial \bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=\hat{\Omega}} > 0\ \forall \hat{\Omega} \in [0,1]$), an increase in participation of sex-i individuals results in other sex-i individuals being relatively disincentivized to participate in warfare and individuals of the other sex being relatively incentivized to participate in warfare, that is $\partial\theta_{\mathrm{i}}/\partial\bar{\Omega}_{\mathrm{i}} < \partial\theta_{\mathrm{j}}/\partial\bar{\Omega}_{\mathrm{i}}$ (see also Fig. 3.1a). Specifically, three cases are possible: if $\partial\theta_{\mathrm{i}}/\partial\bar{\Omega}_{\mathrm{i}} > 0$ and $\partial\theta_{\mathrm{j}}/\partial\bar{\Omega}_{\mathrm{i}} > 0$, an increase in participation of sex-i individuals promotes further participation of individuals of the same sex less than participation of individuals of the other sex; if $\partial\theta_{\mathrm{i}}/\partial\bar{\Omega}_{\mathrm{i}} < 0$ and $\partial\theta_{\mathrm{j}}/\partial\bar{\Omega}_{\mathrm{i}} > 0$, an increase in participation of sex-i individuals inhibits further participation of individuals of the same sex and promotes participation of individuals of the other sex; if $\partial\theta_{\mathrm{i}}/\partial\bar{\Omega}_{\mathrm{i}} < 0$ and $\partial\theta_{\mathrm{j}}/\partial\bar{\Omega}_{\mathrm{i}} < 0$, an increase in participation of sex-i individuals inhibits further participation of individuals of the same sex more than participation of individuals of the other sex.

Analogously, if costs are decelerating ($\partial c(\bar{\Omega}_{\mathrm{i}})/\partial\bar{\Omega}_{\mathrm{i}}|_{\bar{\Omega}_{\mathrm{i}}=\hat{\Omega}} < 0\ \forall\hat{\Omega} \in [0,1]$), an increase in participation of sex-i individuals results in other sex-i individuals being relatively incentivized to participate in warfare and individuals of the other sex being relatively disincentivized to participate in warfare, that is $\partial\theta_{\mathrm{i}}/\partial\bar{\Omega}_{\mathrm{i}} > \partial\theta_{\mathrm{j}}/\partial\bar{\Omega}_{\mathrm{i}}$ (see also Fig. 3.1b). Specifically, three cases are possible: if $\partial\theta_{\mathrm{i}}/\partial\bar{\Omega}_{\mathrm{i}} > 0$ and $\partial\theta_{\mathrm{j}}/\partial\bar{\Omega}_{\mathrm{i}} > 0$, an increase in participation of sex-i individuals promotes further participation of individuals of the same sex more than participation of individuals of the other sex; if $\partial\theta_{\mathrm{i}}/\partial\bar{\Omega}_{\mathrm{i}} > 0$ and $\partial\theta_{\mathrm{j}}/\partial\bar{\Omega}_{\mathrm{i}} < 0$, an increase in participation of sex-i individuals promotes further participation of individuals of the same sex and inhibits participation of individuals of the other sex; if $\partial\theta_{\mathrm{i}}/\partial\bar{\Omega}_{\mathrm{i}} < 0$ and $\partial\theta_{\mathrm{j}}/\partial\bar{\Omega}_{\mathrm{i}} < 0$, an increase in participation of sex-i individuals inhibits further participation of individuals of the same sex less than participation of individuals of the other sex.

Participation equilibria in the context of other sex differences in the ecology of war

Consider now a case in which there may be sex differences in the ecology of warfare other than differences in participation.

ACCELERATING COSTS

We demonstrate that, in the case in which personal costs are accelerating, and the benefits, or personal costs, or migration rates, or admixture coefficients are not equal for the two sexes, a population with equal participation of the two sexes – i.e. a point on the diagonal, excluding the extremes – cannot be in a stable equilibrium, and therefore it will be pushed off of the diagonal. In addition, a difference in in one of the four ecological parameters listed above is sufficient condition for $\Omega_{\mathrm{i}}^{*} \geq \Omega_{\mathrm{j}}^{*}$ or $\Omega_{\mathrm{i}}^{*} \leq \Omega_{\mathrm{j}}^{*}$, where Ω_{i}^{*} is the stable level of participation for sex $\mathrm{i} \in \{\mathrm{m,f}\}$. We consider four cases in turn:

i) $b_\mathrm{i}(\Omega_\mathrm{i}, \Omega_\mathrm{j}) \neq b_\mathrm{j}(\Omega_\mathrm{i}, \Omega_\mathrm{j})$, and $c_\mathrm{i}(\Omega_\mathrm{i}) = c(\Omega_\mathrm{i})$, $m_\mathrm{i} = m$, $s_\mathrm{i} = s$, which implies $M_\mathrm{i} = M$, for all $\mathrm{i} \in \{\mathrm{m,f}\}$; considering a population characterized by $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$, the marginal fitness function for participation of sex i is $\theta_\mathrm{i} = 4(1-s)rb_\mathrm{i}(\tilde{\Omega}, \tilde{\Omega}) - (1-(1-2\varpi M)r)c(\tilde{\Omega})$. If $b_\mathrm{i} > b_\mathrm{j}$, then $\theta_\mathrm{i} > \theta_\mathrm{j}$ for every possible value of $\tilde{\Omega}$, which implies $\Omega_\mathrm{i}^* \geq \Omega_\mathrm{j}^*$.

ii) $c_\mathrm{i}(\Omega_\mathrm{i}) \neq c_\mathrm{j}(\Omega_\mathrm{i})$ and $b_\mathrm{i}(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{j}, \Omega_\mathrm{i})$, $m_\mathrm{i} = m$, $s_\mathrm{i} = s$, which implies $M_\mathrm{i} = M$, for all $\mathrm{i} \in \{\mathrm{m,f}\}$; considering a population characterized by $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$, the marginal fitness function for participation of sex i is $\theta_\mathrm{i} = 4(1-s)rb(\tilde{\Omega}, \tilde{\Omega}) - (1-(1-2\varpi M)r)c_\mathrm{i}(\tilde{\Omega})$. If $c_\mathrm{i} < c_\mathrm{j}$, then $\theta_\mathrm{i} > \theta_\mathrm{j}$ for every possible value of $\tilde{\Omega}$, which implies $\Omega_\mathrm{i}^* \geq \Omega_\mathrm{j}^*$.

iii) $m_\mathrm{i} \neq m_\mathrm{j}$ and $b_\mathrm{i}(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{j}, \Omega_\mathrm{i})$, $c_\mathrm{i}(\Omega_\mathrm{i}) = c(\Omega_\mathrm{i})$, $s_\mathrm{i} = s$, which implies $M_\mathrm{i} = M$, for all $\mathrm{i} \in \{\mathrm{m,f}\}$; considering a population characterized by $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$, the marginal fitness function for participation of sex i is $\theta_\mathrm{i} = 2\left((1-s)(r_\mathrm{ii} + r_\mathrm{ij})\right)b(\tilde{\Omega}, \tilde{\Omega}) - (1-(1-2\varpi M)r_\mathrm{ii})c_\mathrm{i}(\tilde{\Omega})$, where $r_\mathrm{ii} = (1-m_\mathrm{i})^2 r_\mathrm{x}$ and $r_\mathrm{ij} = (1-m_\mathrm{i})(1-m_\mathrm{j})r_\mathrm{x}$. If $m_\mathrm{i} < m_\mathrm{j}$, then $\theta_\mathrm{i} > \theta_\mathrm{j}$ for every possible value of $\tilde{\Omega}$, which implies $\Omega_\mathrm{i}^* \geq \Omega_\mathrm{j}^*$.

iv) $M_\mathrm{i} \neq M_\mathrm{j}$ and $b_\mathrm{i}(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{j}, \Omega_\mathrm{i})$, $c_\mathrm{i}(\Omega_\mathrm{i}) = c(\Omega_\mathrm{i})$, $m_\mathrm{i} = m$, for all $\mathrm{i} \in \{\mathrm{m,f}\}$; considering a point on the diagonal $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$, the marginal fitness function for participation of sex i is $\theta_\mathrm{i} = 2\left((1-s_\mathrm{i}) + (1-s_\mathrm{j})\right)rb(\tilde{\Omega}, \tilde{\Omega}) - (1-(1-2\varpi M_\mathrm{i})r)c(\tilde{\Omega})$. If $M_\mathrm{i} < M_\mathrm{j}$, then $\theta_\mathrm{i} > \theta_\mathrm{j}$ for every possible value of $\tilde{\Omega}$, which implies $\Omega_\mathrm{i}^* \geq \Omega_\mathrm{j}^*$.

DECELERATING COSTS

We demonstrate that, in the case in which personal costs are decelerating, and the benefits, or personal costs, or migration rates, or admixture coefficients are not equal for the two sexes, a population with equal participation of the two sexes – i.e. a point on the diagonal, excluding the extremes – cannot be a stable equilibrium, and therefore it will be pushed off of the diagonal. This implies that, in the case in which two single-sex equilibria exist, the diagonal is contained in one of the two subspaces of initial conditions leading to such equilibria and therefore the two subspaces (basins of attraction) are of unequal size. We consider four cases in turn:

i) $b_i(\Omega_i, \Omega_j) \neq b_j(\Omega_i, \Omega_j)$, and $c_i(\Omega_i) = c(\Omega_i)$, $m_i = m$, $s_i = s$, which implies $M_i = M$, for all $i \in \{m,f\}$; considering a population characterized by $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$, the marginal fitness function for participation of sex i is $\theta_i = 4(1-s)rb_i(\tilde{\Omega}, \tilde{\Omega}) - (1-(1-2\bar{\omega}M)r)c(\tilde{\Omega})$. If $b_i > b_j$, then $\theta_i > \theta_j$ for every possible value of $\tilde{\Omega}$, and in this case selection will drive the population off of the diagonal, and specifically towards the sex-i-only equilibrium, which implies that the basin of attraction for the sex-i-only equilibrium encompasses the diagonal and is therefore larger than the basin of attraction for the equilibrium where only the other sex participates.

ii) $c_i(\Omega_i) \neq c_j(\Omega_i)$ and $b_i(\Omega_i, \Omega_j) = b(\Omega_i, \Omega_j) = b(\Omega_j, \Omega_i)$, $m_i = m$, $s_i = s$, which implies $M_i = M$, for all $i \in \{m,f\}$; considering a population characterized by $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$, the marginal fitness function for participation of sex i is $\theta_i = 4(1-s)rb(\tilde{\Omega}, \tilde{\Omega}) - (1-(1-2\bar{\omega}M)r)c_i(\tilde{\Omega})$. If $c_i < c_j$, then $\theta_i > \theta_j$ for every possible value of $\tilde{\Omega}$, and in this case selection will drive the population off of the diagonal, and specifically towards the sex-i-only equilibrium, which implies that the basin of attraction for the sex-i-only equilibrium encompasses the diagonal and is therefore larger than the basin of attraction for the equilibrium where only the other sex participates. N.B. $c_i < c_j$ also results in a decrease in the indirect-fitness benefit sex-i individuals accrue via lost reproductive opportunities in their home group being taken by their groupmates of the same sex (relaxation of kin competition; see second term in condition [3.1]). However, this benefit never outweighs the direct inclusive fitness cost associated with a loss of competitiveness (first term in condition [3.1]) and therefore lower personal costs for sex-*i* individuals always lead to the sex-i-only outcome being more likely.

iii) $m_\mathrm{i} \neq m_\mathrm{j}$ and $b_\mathrm{i}(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{j}, \Omega_\mathrm{i})$, $c_\mathrm{i}(\Omega_\mathrm{i}) = c(\Omega_\mathrm{i})$, $s_\mathrm{i} = s$, which implies $M_\mathrm{i} = M$, for all $\mathrm{i} \in \{\mathrm{m,f}\}$; considering a population characterized by $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$, the marginal fitness function for participation of sex i is $\theta_\mathrm{i} = 2\left((1-s)(r_\mathrm{ii} + r_\mathrm{ij})\right) b(\tilde{\Omega}, \tilde{\Omega}) - (1 - (1 - 2\overline{\omega} M) r_\mathrm{ii}) c_\mathrm{i}(\tilde{\Omega})$, where $r_\mathrm{ii} = (1 - m_\mathrm{i})^2 r_\mathrm{x}$ and $r_\mathrm{ij} = (1 - m_\mathrm{i})(1 - m_\mathrm{j}) r_\mathrm{x}$. If $m_\mathrm{i} < m_\mathrm{j}$, then $\theta_\mathrm{i} > \theta_\mathrm{j}$ for every possible value of $\tilde{\Omega}$, and in this case selection will drive the population off of the diagonal, and specifically towards the sex-i-only equilibrium, which implies that the basin of attraction for the sex-i-only equilibrium encompasses the diagonal and is therefore larger than the basin of attraction for the equilibrium where only the other sex participates.

iv) $M_\mathrm{i} \neq M_\mathrm{j}$ and $b_\mathrm{i}(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{i}, \Omega_\mathrm{j}) = b(\Omega_\mathrm{j}, \Omega_\mathrm{i})$, $c_\mathrm{i}(\Omega_\mathrm{i}) = c(\Omega_\mathrm{i})$, $m_\mathrm{i} = m$, for all $\mathrm{i} \in \{\mathrm{m,f}\}$; considering a point on the diagonal $(\tilde{\Omega}, \tilde{\Omega})$ with $\tilde{\Omega} \neq 0{,}1$, the marginal fitness function for participation of sex i is $\theta_\mathrm{i} = 2\left((1 - s_\mathrm{i}) + (1 - s_\mathrm{j})\right) r b(\tilde{\Omega}, \tilde{\Omega}) - (1 - (1 - 2\overline{\omega} M_\mathrm{i}) r) c(\tilde{\Omega})$. If $M_\mathrm{i} < M_\mathrm{j}$, then $\theta_\mathrm{i} > \theta_\mathrm{j}$ for every possible value of $\tilde{\Omega}$, and in this case selection will drive the population off of the diagonal, and specifically towards the sex-i-only equilibrium, which implies that the basin of attraction for the sex-i-only equilibrium encompasses the diagonal and is therefore larger than the basin of attraction for the equilibrium where only the other sex participates.

Illustrations: war outcome functions

For the purposes of illustration alone (Fig. 3.1,3.2) we make the war outcome functions explicit Notice that the results presented in this study and especially conditions [3.1-3.3] do not hinge on any particular functionalisation. We consider that the probability that the attacking group wins the war ω is a function of the fighting strengths σ_att and σ_def of the attacking and defending groups, specifically $\omega = \sigma_\mathrm{att} / (\sigma_\mathrm{att} + \sigma_\mathrm{def})$. We consider that the fighting strengths of the two groups are themselves functions of a) the number of fighting individual of the two sexes, that is $N \cdot K \cdot \Omega_\mathrm{i,att}$ and $N \cdot K \cdot \Omega_\mathrm{i,def}$ (for the attacking and defending groups, respectively, assuming equal numbers of adults of the two sexes N_m=N_f=N) and b) the fighting effectiveness of the two sexes (ψ_i, for all i∈{m,f}). Considering that groups do not differ in total size and there are equal numbers of young adults of the two sexes and therefore only the proportions of fighting individuals of the two sexes influence the final outcome, we assume functional form $\sigma_{att} = ½ (\psi_i\ \Omega_{i,att} + \psi_j\ \Omega_{j,att})$ and $\sigma_{def} = ½ (\psi_i\ \Omega_{i,def} + \psi_j\ \Omega_{j,def})$.

4 Sex differences in altruism and the demography of human warfare

> […] readiness to behave altruistically to the benefit of in-group members (‘in-group love’) and to act hostilely toward out-groups (‘out-group hate’) have been closely linked in human evolution.
>
> –Hannes Rusch (2014)

Abstract

Recent years have seen an increasing interest in understanding possible links between warfare and the high levels of within-group altruism observed in human societies. At the same time, sex has been shown to modulate incentives to express social behaviours in populations characterised by warfare demographies. However, the potential for sex differences in altruism in the context of warfare has been relatively neglected and the possibility that such differences might be driven by sex biases in demography has not been explored formally. Here, we develop a kin selection model to investigate how the sex of the

altruist and that of the beneficiary influences patterns of such behaviours in populations that experience between-group conflict. We find that sex is a fundamental modulator of altruism in the context of the demography of warfare: members of the sex that competes more globally and/or is more philopatric are favoured to behave more altruistically towards same-sex groupmates than opposite-sex ones. The effects of these two factors may reinforce each other, potentially explaining recently-observed patterns of sex-specific altruism in populations with different post-marital dispersal norms.

Introduction

Recent years have seen strong interest in understanding possible links between warfare – that is, 'coalitionary intergroup aggression' in its broadest definition (Wrangham, 1999; Choi and Bowles, 2007) – and the high levels of within-group altruism observed in human societies (reviewed in Rusch, 2014). The possibility that between-group violence might have influenced the evolution of within-group altruism was first suggested by Darwin (1871). In the last decade, this argument has received renewed attention, especially thanks to an influential modelling study on this subject by Choi and Bowles (2007), who proposed the term 'parochial altruism' for the intersection of hostility towards other groups and within-group altruism. Specifically, this and other evolutionary models (Bowles, 2006, 2009; Choi and Bowles, 2007; Garcia and van der Bergh, 2011) have demonstrated that there can be selection for altruism towards groupmates – i.e. any behaviour that benefits the recipients and determines a cost for the carrier – in populations experiencing intergroup warfare. Further, archaeological and ethnographic evidence suggests that prehistoric wars were frequent and violent enough to favour the evolution and maintenance of the high levels of within-group altruism observed in human societies (reviewed in Bowles, 2009).

At the same time, an increasing body of literature is starting to suggest that sex might be an important modulator of social behaviours in populations experiencing intergroup warfare, including its demographic consequences (e.g. movement of individuals between groups as a result of victory or defeat). For instance, proponents of the ‘male warrior hypothesis’ suggest that intergroup warfare has exerted selective pressures leading to psychological sex differences – with males cooperating with other males to attack individuals in other groups and obtain reproductive opportunities, and women avoiding sexual coercion from foreign males (van Vugt, et al., 2006; van Vugt, 2009). Some empirical evidence supporting this hypothesis is available (reviewed in McDonald, et al., 2012). For example, men are more aggressive than women when their group is under threat in experimental wargames (Johnson, et al., 2006). Also, in economic games, men donate more to ingroup members – i.e. they are more cooperative – when the group is in competition with another group, while this makes no difference for women’s behaviour (but notice that, overall, women donate more than men; van Vugt, et al., 2006).

Moreover, a recent kin-selection model of warfare has found that fathers and mothers differ in their incentives to push their sons to initiate and participate in wars – and such differences are driven by relatedness asymmetries, which may result from sex biases in dispersal (Micheletti, et al., 2017; Chapter 2). In addition, male and female behaviours in the context of war can interact in surprising ways. For example, an evolutionary feedback between male and female participation in warfare – possibly reinforced by female-biased dispersal – has been suggested to have driven the near-total absence of women from the battlefield until very recent times (Micheletti, et al., 2018; Ch.3).

Furthermore, a recent study of cooperation and altruism patterns in several small-scale, traditional Sino-Tibetan societies – that have a past of intergroup conflict and cattle raiding (R. Mace, pers. comm.) – has shown that men are more cooperative than women in dictator, public goods, and resource dilemma games (Wu, et al., 2015). Further, the same study has shown that overall levels of cooperation and altruism within social groups vary with post-marital residence systems – that is, depending on which sex, if any, migrates to the spouse's social group at marriage (patrilocality if women move; matrilocality if men move; and duolocality if neither sex moves).

However, potential sex differences in altruism in populations experiencing intergroup warfare have been relatively neglected in theoretical studies within the parochial altruism literature mentioned above, with mathematical models not considering separate sexes (Bowles, 2006, 2009; Choi and Bowles, 2007; Garcia and van der Bergh, 2011). In particular, while parochial altruism theory suggests that it is the demography of warfare that drives cooperative behaviours – with populations subdivided into groups engaging in aggressive interactions – existing literature has neglected the possibility that sex biases in demographic parameters might drive sex differences in altruistic behaviours (that is, those behaviours that determine a decrease in the competitiveness for reproductive opportunities of the altruist and an increase in that of the recipient). Moreover, levels of altruism might depend on the sex of the beneficiary of altruism, as well as on the sex of the altruist – that is, the sex of both interactants may determine behavioural patterns. Since men and women in human populations often have different evolutionary interests and play different roles in social groups (Low, 2015), illuminating the potential for sex differences in altruism and possible demographic drivers is key for increasing our understanding of human sociality.

Here, we assess the scope for the demography of warfare – i.e. the movement of individuals between groups as a result of warfare – and of sex differences in demographic parameters to influence patterns of sex-specific, within-group altruism. We define altruism broadly, as any behaviour that reduces the competitiveness for reproductive opportunities of the actor, but raises the competitiveness of the recipient (Hamilton, 1964; West, et al., 2007a). Such altruism may be realised in a number of ways: for example, helping an individual with foraging or farm work, donating or sharing fitness-enhancing resources like food, tools, or shelter. We expand a previously developed two-sex kin-selection model of between-group conflict (Lehmann and Feldman, 2008; Micheletti, et al., 2017, 2018; Chapters 2 and 3) to investigate the evolution of altruism performed by men and women towards either male groupmates or female groupmates. We thus consider four altruistic behaviours: male-to-male altruism, male-to-female altruism, female-to-male altruism, and female-to-female altruism. We focus on the effects of sex differences in two demographic parameters: sex-specific rates of dispersal and fractions of reproductive opportunities obtained through inter-group conflict by conquering men and conquering women and taken from conquered groups.

Methods

We consider the evolution of within-group altruism in the context of warfare, by adapting and expanding a previously-developed model of coalitionary intergroup conflicts (Lehmann and Feldman, 2008; Micheletti, et al., 2017, 2018; Chapter 2 and 3). In order to explore how sex might modulate this behaviour, we consider four altruistic traits: male-to-male altruism (x_{mm}), male-to-female altruism (x_{mf}), female-to-male altruism (x_{fm}), and female-to-female altruism (x_{ff}).

Following Lehmann and Feldman (2008) and Micheletti, et al. (2017, 2018; Chapters 2 and 3), we consider a large population subdivided into groups of N_{i} adults of sex $\mathrm{i} \in \{\mathrm{m},\mathrm{f}\}$. At the beginning of the life cycle, each adult female produces a large number K_{i} of sex i offspring, who mature to become young adults (for simplicity and following Lehmann and Feldman (2008) and Micheletti, et al. (2017, 2018; Chapters 2 and 3) we assume non-overlapping generations, so that only young adults – hereafter 'individuals' – can disperse, be altruistic and reproduce). Each sex-i individual may then disperse to a randomly-chosen group with sex-specific probability m_{i}. After the dispersal phase, individuals have the opportunity to be altruistic towards groupmates of the same sex (x_{ii}) or the opposite sex (x_{ij}; where $\mathrm{j} \in \{\mathrm{m},\mathrm{f}\}$ and $\mathrm{j} \neq \mathrm{i}$). The war phase follows, with each post-dispersal group having the chance to attack another group with probability a and be attacked by a third group, with the same probability a – and attackers winning the war with probability ω. Individuals then compete for reproductive opportunities (density-dependent regulation phase). In groups that are not attacked or that are attacked and successfully defend themselves, sex-i individuals compete only with sex-i groupmates and have competitiveness t_{i}, which is the individual's basic competitiveness. Instead, in groups that are attacked and are defeated by their attackers, sex-i individuals compete for reproductive opportunities with both sex-i groupmates and with their sex-i attackers, with the conquered group's sex-i individuals having competitiveness for reproductive opportunities $(1 - \sigma_{\mathrm{i}})\, t_{\mathrm{i}}$ and the conquering group's sex-i individuals having competitiveness $\sigma_{\mathrm{i}}\, t_{\mathrm{i}}$ – where the competitiveness modifier σ_i is equal to the fraction of sex-i reproductive opportunities in a conquered group seized by conquering sex-i individuals. The basic competitiveness t_i of a sex-i individual is modulated by the altruism performed by that sex-i individual towards sex-j individuals ($x_{ij,ind}$) and towards other sex-i individuals ($x_{ii,ind}$) and the altruism the sex-i individual receives from sex-j individuals ($x_{ji,grp}$) and from other sex-i individuals ($x_{ii,grp}$) in their group; such that $-(\partial t_i/\partial x_{ij,ind})/\bar{t}_i = c_{ij}$ is the competitive cost of being altruistic towards sex-j groupmates incurred by the sex-i individual, $-(\partial t_i/\partial x_{ii,ind})/\bar{t}_i = c_{ii}$ is the competitive cost of being altruistic towards sex-i groupmates incurred by the sex-i individual, $(\partial t_i/\partial x_{ji,grp})\,/\bar{t}_i = (\partial t_j/\partial x_{ij,grp})\,/\bar{t}_j = b_{ij}$ is the marginal increase in competitiveness enjoyed by the sex-i individual as a result of altruism received from sex-j groupmates, $(\partial t_i/\partial x_{ii,grp})\,/\bar{t}_i = b_{ii}$ is the marginal increase in competitiveness enjoyed by the sex-i individual as a result of altruism received from sex-i groupmates (see Extended Methods for details).

Results

Analysing the model, we find that natural selection – including both direct and indirect (i.e. kin selection) effects (Hamilton, 1964; Maynard Smith, 1964; Taylor, 1996; Taylor and Frank 1996; Frank 1997, 1998; Rousset, 2004; Taylor, et al., 2007) – favours an individual of sex i ∈ {m,f} to increase their altruism towards opposite-sex groupmates when:

$$-c_{ij} + \alpha_i c_{ij} r_{ii} + b_{ij} r_{ij} - \alpha_j b_{ij} r_{ij} > 0, \qquad [4.1]$$

where c_{ij} is the marginal cost incurred by the sex-i individual on account of their altruism towards groupmates of the opposite sex, j; b_{ij} is the marginal benefit enjoyed by the opposite-sex recipient of the altruistic act performed by the sex-i individual; r_{ij} is the genetic relatedness between groupmates of opposite sexes; r_{ii} is the genetic relatedness between groupmates of the same sex i; and $\alpha_i = 1 - 2a\omega(1 - \sigma_i)\sigma_i$ is the extent to which individuals of sex i compete for reproductive opportunities with same-sex groupmates (i.e. 'locally') as opposed to individuals in other groups (i.e. 'globally'). That is, by increasing their level of altruism towards members of the opposite sex, an individual of sex i incurs: a direct-fitness cost (first term in condition [4.1]) owing to a $-c_{ij}$ loss of competitiveness for reproductive opportunities; an indirect-fitness benefit (second term) owing to a corresponding relaxation of kin competition in their own sex, as c_{ij} reproductive opportunities become available to sex-i individuals who are competing kin with probability α_i and who are related to the focal individual by r_{ii}; an indirect-fitness benefit (third term) owing to a b_{ij} increase in competitiveness for reproductive opportunities for individuals of the opposite sex who are related to the focal sex-i individual by r_{ij}; an indirect-fitness cost (fourth term) owing to a corresponding increase in kin competition, as fewer reproductive opportunities ($-b_{ij}$) are available for individuals of the opposite sex who are derived from the same group – and are thus competing kin – with probability α_j, and who are related to the focal individual by r_{ij}. Note that condition [4.1] holds even when individuals gain a direct benefit from performing the behaviour ($c_{ij} < 0$), in which case this constitutes mutual benefit rather than altruism (West, et al., 2007; the results of the present analysis thus hold for cooperative behaviours in general, i.e. including both altruism and mutual benefit).

Condition [4.1] may be rearranged into the form $c_{ij}/b_{ij} < A_{ij}$, where

$$A_{\mathrm{ij}} = \frac{r_{\mathrm{ij}} - \alpha_{\mathrm{j}} r_{\mathrm{ij}}}{1 - \alpha_{\mathrm{i}} r_{\mathrm{ii}}} \qquad [4.2]$$

is the ‘potential for altruism’ by members of sex i towards opposite-sex groupmates (cf. Gardner, 2010). This approach separates the cost and benefit functions ($c_{\mathrm{ij}}/b_{\mathrm{ij}}$; left-hand side of the rearranged condition) from demographic effects on altruism (the ‘potential’ A_{ij}; right-hand side). By analysing potentials for altruism, it is possible to investigate sex-specific effects of demography on altruism – the aim of the present study – independently of sex differences in the cost and benefits functions, which do not derive from sex-differences in demography.

Further, we find that natural selection favours an individual of sex i ∈ {m,f} to increase their altruism towards same-sex groupmates when:

$$-c_{\mathrm{ii}} + \alpha_{\mathrm{i}} c_{\mathrm{ii}} r_{\mathrm{ii}} + b_{\mathrm{ii}} r_{\mathrm{ii}} - \alpha_{\mathrm{i}} b_{\mathrm{ii}} r_{\mathrm{ii}} > 0, \qquad [4.3]$$

where c_{ii} is the marginal cost incurred by the sex-i individual on account of their altruism towards groupmates of the same sex; and b_{ii} is the marginal benefit enjoyed by the same-sex recipient of the altruistic act performed by the sex-i individual.

Condition [4.3] can be rearranged into the form $c_{\mathrm{ii}}/b_{\mathrm{ii}} < A_{\mathrm{ii}}$, where

$$A_{\mathrm{ii}} = \frac{r_{\mathrm{ii}} - \alpha_{\mathrm{i}} r_{\mathrm{ii}}}{1 - \alpha_{\mathrm{i}} r_{\mathrm{ii}}} \qquad [4.4]$$

is the ‘potential for altruism’ by members of sex i towards same-sex groupmates.

Consideration of potentials for altruism (equations [4.2] and [4.4]) reveals two key results. First, all else being equal, the more philopatric sex (i.e. characterised by a lower dispersal rate) has a greater potential for altruism towards the same sex than towards the opposite sex, whereas the less philopatric sex has a greater potential for altruism towards the opposite sex than towards the same sex (see Fig. 4.1a,e,i). For example, in the case of female-biased dispersal ($m_{\mathrm{m}} < m_{\mathrm{f}}$), we predict that both men and women are more altruistic towards male groupmates than towards female groupmates. This is because, being more philopatric, men are more related to both men and women in the group than women are ($r_{\mathrm{mm}} > r_{\mathrm{mf}} > r_{\mathrm{ff}}$) and thus the benefits reaped by actors of both sexes from being altruistic towards men are higher.

Second, all else being equal, the sex characterised by a higher degree of admixture – that is the sex that, in a conquered group, shares reproductive opportunities with members of the other group to a greater extent ($M_{\mathrm{i}} = (1 - \sigma_{\mathrm{i}})\sigma_{\mathrm{i}}$; Micheletti, et al., 2017; Chapter 2) – has a higher potential for altruism towards groupmates of the same sex than towards those of the opposite sex, whereas the sex characterised by a lower degree of admixture has a higher potential for altruism towards the opposite sex than the same sex (see Fig. 4.1, ‘unbiased dispersal’ dividing line). This is because, for the higher-admixture sex, competition for reproductive opportunities is relatively more global (lower α_{i}) whereas, for the lower-admixture sex, competition is relatively more local (higher α_{i}).

Consider, for example, the case in which only men participate in warfare and, if they win, they obtain some reproductive success in the conquered group, but women from the conquering group do not ($\sigma_{\mathrm{m}} \neq 0,1$; $\sigma_{\mathrm{f}} = 0$). Men have thus higher admixture ($M_{\mathrm{m}} > M_{\mathrm{f}} = 0$), meaning that competition is relatively more global for them than for women ($\alpha_{\mathrm{m}} < \alpha_{\mathrm{f}}$).

As a consequence, both sexes are altruistic towards men, but not towards women (see Fig. 4.1b,c). If, instead, women obtain some reproductive success in the conquered group – because, for example, they have the opportunity to accompany conquering men after victory – but do so to a lesser extent than men (e.g. σ_{m}, $\sigma_{\mathrm{f}} < 0.5$, $\sigma_{\mathrm{m}} > \sigma_{\mathrm{f}} \neq 0$, $M_{\mathrm{m}} > M_{\mathrm{f}} \neq 0$), then now both sexes are altruistic towards women, but still less so than they are towards men (see Fig. 4.1, 'unbiased dispersal' dividing line).

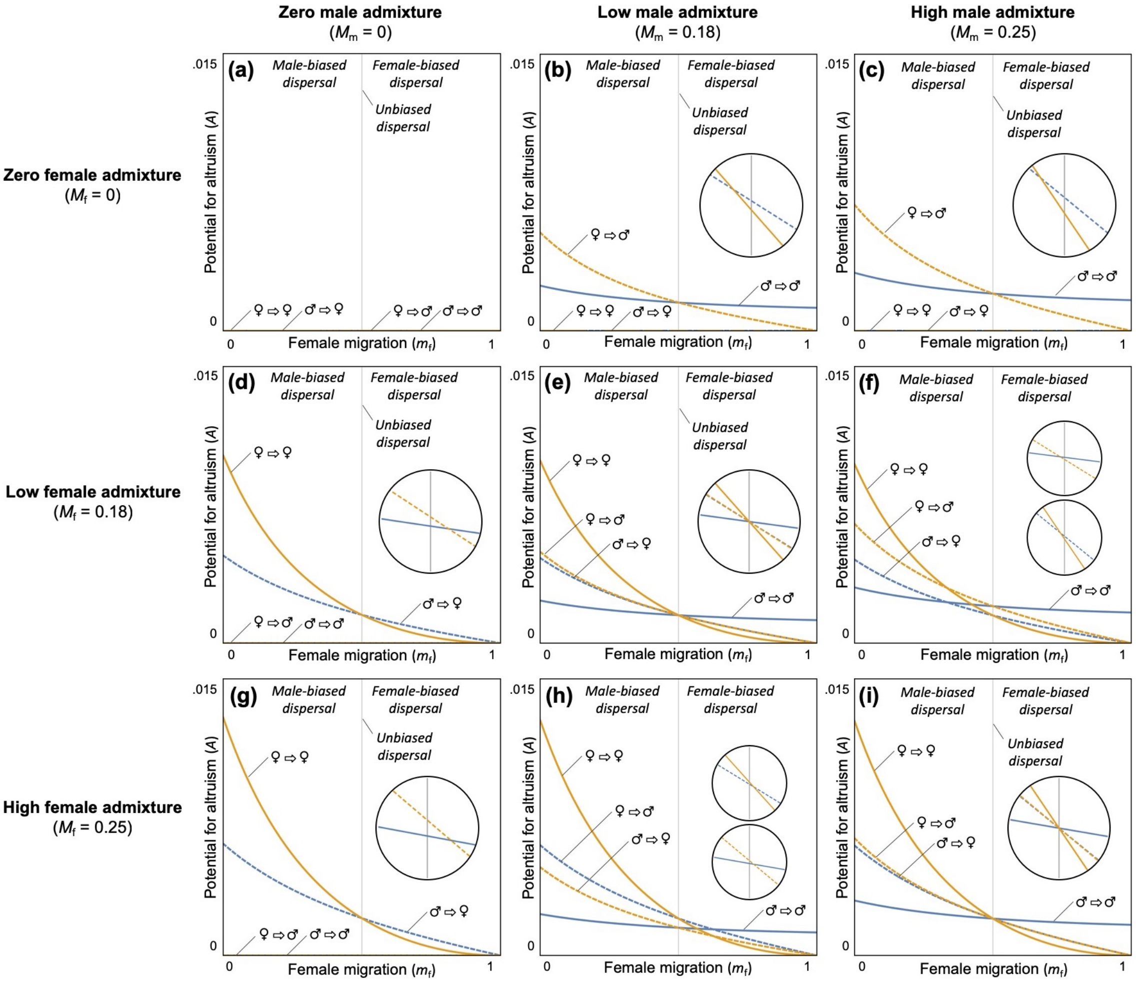

Figure 4.1 – Potentials for altruism performed by men or women and directed towards men or women as a function of female dispersal, for zero, low, and high values of male and female admixture. Other parameter values: $N_{\mathrm{m}} = N_{\mathrm{f}} = 10$, $a = 0.5$, $\omega = 0.5$, $m_{\mathrm{m}} = 0.5$ (male-biased dispersal $m_{\mathrm{m}} > m_{\mathrm{f}}$; unbiased dispersal; $m_{\mathrm{m}} = m_{\mathrm{f}}$; female-biased dispersal $m_{\mathrm{m}} < m_{\mathrm{f}}$).

Moreover, we find that the effects of sex biases in admixture and in dispersal – the two key modulators of altruism in the context of warfare we have identified above – may reinforce each other or act in different directions. Specifically, if male admixture is higher than female admixture ($M_m > M_f$) then: under male-biased dispersal ($m_m > m_f$), patterns depend on parameter values, as the sex bias in admixture acts towards greater potential for altruism towards men, while the sex bias in dispersal acts towards greater potential for altruism towards women; under unbiased dispersal ($m_m = m_f$) men receive more help than women, from both sexes; under female-biased dispersal ($m_m < m_f$) both sexes help men more than women, as both effects act towards greater potential for altruism towards men (see Fig 4.1f). Mirroring patterns are obtained if male admixture is lower than female admixture ($M_m < M_f$): under male-biased dispersal ($m_m > m_f$) both sexes help women more than men, as both effects act towards greater potential for altruism towards women; under unbiased dispersal ($m_m = m_f$) women receive more help than men, from both sexes; under female-biased dispersal ($m_m < m_f$) patterns depend on parameter values, as the sex bias in admixture acts towards greater potential for altruism towards women, while the sex bias in dispersal is acts towards greater potential for altruism towards men (see Fig. 4.1h) (see Extended Methods for details).

So far, we have considered how potentials for altruism vary for the two sexes and with sex biases in demographic parameters. However, whether altruism actually evolves and to what level also depends on the cost and benefit functions. Thus, levels of altruism – if they settle at some intermediate, convergence-stable level (Taylor, 1996; Davies, et al., 2016) – are given by setting the left-hand side of conditions for increase [4.1] and [4.3] to zero and solving for x_{ij}^* and x_{ii}^*, respectively. Members of the sex that competes relatively more globally ($\alpha_i < \alpha_j$, owing to $M_i > M_j$) and/or is more philopatric ($m_i < m_j$) are favoured to express higher levels of altruism towards same-sex than opposite-sex groupmates (see Fig. 4.2) – if assuming that (a) there are no sex differences in costs and benefits; (b) the effects of different altruistic behaviours on competitiveness for reproductive opportunities are multiplicative, so that the four traits under consideration do not influence each other (see Extended Methods for details). Notice that these results are qualitatively identical to those revealed by the analysis of potentials for altruism (see Fig. 4.1).

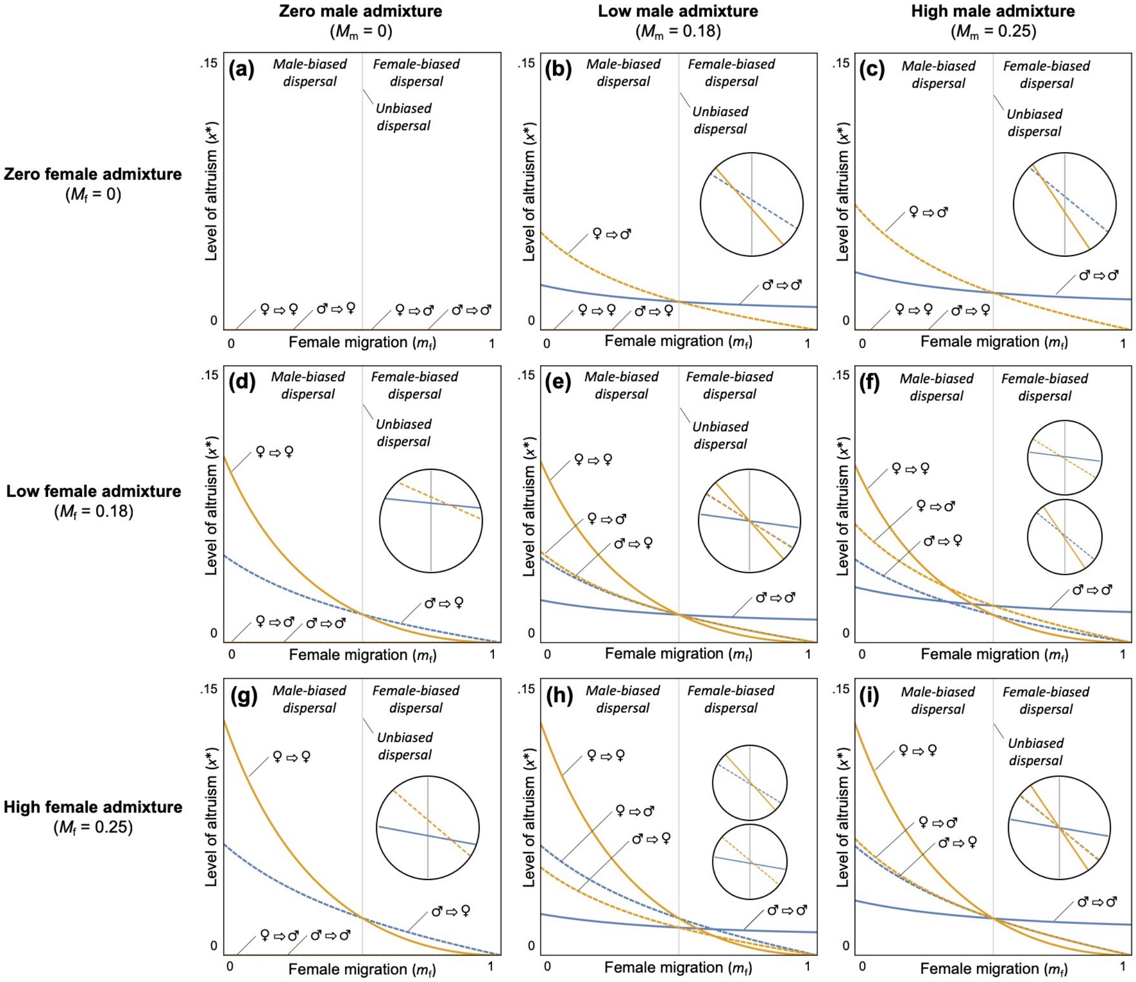

Figure 4.2 – Convergence-stable level of altruism performed by men or women and directed towards men or women as a function of female dispersal, for zero, low, and high values of male and female admixture. For the purposes of illustration we assume functional forms: $t_{i,ind} = (1 - \chi x_{ii,ind})(1 - \chi x_{ij,ind}) x_{ii,grp} x_{ji,grp}$ with $\chi = 0.1$. Other parameter values: $N_m = N_f = 10$, $a = 0.5$, $\omega = 0.5$, $m_m = 0.5$ (male-biased dispersal $m_m > m_f$; unbiased dispersal; $m_m = m_f$; female-biased dispersal $m_m < m_f$).

Discussion

Investigation of the possible links between warfare and within-group altruism in human societies has developed rapidly in the past decade (reviewed in Rusch, 2014). At the same time, a number of studies have suggested that sex might modulate social behaviours in populations that experience or have experienced between-group coalitionary aggression (Johnson, et al., 2006; van Vugt, et al., 2006; van Vugt, 2006; McDonald, et al., 2012; Wu, et al., 2015; Micheletti, et al., 2017, 2018; Chapters 2 and 3). However, the possible role of sex in determining patterns of altruism in the context of warfare has remained unexplored. Here, we developed a kin selection model of altruism performed by men and women towards male or female groupmates, in a population subdivided into groups engaging in warfare, to address this possibility. We found that sex is a fundamental modulator of altruism in a population characterised by between-group aggression: levels of altruism vary with the sex of the altruist and that of the recipient and these differences are driven by sex biases in demographic parameters. Specifically, we found that individuals of the more philopatric sex (i.e. with lower dispersal) are favoured to be more altruistic towards same-sex than opposite-sex groupmates. Moreover, individuals of the sex characterised by a greater degree of admixture – and thus relatively more global competition – are favoured to be more altruistic towards same-sex than opposite-sex groupmates. The effects of these two factors may reinforce each other or act in different directions, so that different combinations of sex-biased dispersal and admixture result in different patterns of altruism.

First, we showed that, all else being equal, female-biased dispersal results in both men and women being more genetically related to male groupmates than female groupmates, thus driving the evolution of higher levels of altruism towards men from both sexes. On the other hand, in societies characterised by male-biased dispersal, individuals of both sexes are more related to female than male groupmates, and are thus favoured to be more altruistic towards the former than the latter. That is, sex biases in migration generate relatedness asymmetries that alter the inclusive fitness benefits of behaving altruistically towards men and women in the context of warfare. In this respect, it is important to underline that, following Lehmann and Feldman (2008) and Micheletti, et al. (2017, 2018; Chapters 2 and 3), we have assumed that altruistic behaviours are performed after dispersal (the same assumption is made in other studies investigating dispersal-altruism interplay outwith the context of warfare; e.g. Johnstone and Cant, 2008). This means that members of the more philopatric sex are more related to their groupmates, but do not experience higher local competition. If, instead, altruistic behaviours were performed before dispersal, then members of the more philopatric sex would experience more local competition (which could possibly outweigh the benefits of being altruistic towards highly-related groupmates).

Second, we showed that, all else being equal, both sexes are favoured to be more altruistic towards the sex characterised by the higher degree of admixture: that is, the sex for which competition is relatively more global. For example, if warfare results in male admixture being higher than female admixture – and consequently competition being relatively more global among men than among women – then both sexes are favoured to behave more altruistically towards men than towards women. This is because, although altruism can improve the competitiveness of both female and male groupmates, the altruist’s female groupmates tend to compete for reproductive opportunities against each other (such that one female relative’s gain is another female relative’s loss), whilst the altruist’s male groupmates are more likely to compete for reproductive opportunities against unrelated individuals in other social groups. For this reason, the returns in terms of inclusive fitness benefits are higher when helping the sex that competes more globally.

Finally, we showed that the effects of these two demographic factors can reinforce each other or act in different directions. We have provided predictions for levels of altruism in populations experiencing warfare for different combinations of sex biases in admixture and in migration. For example, if male admixture is lower than female admixture – consistent, for instance, with men obtaining all reproductive spots in the conquered group and women only a fraction ($\sigma_m = 1$, $\sigma_f \neq 0,1$, $M_m < M_f$) – and dispersal is either unbiased or female-biased, then men are favoured to be more altruistic than women towards a given sex (cf. Johnstone and Cant (2008) who find that the more philopatric sex can be favoured to help more than the other sex).

We thus offer a potential explanation for the finding of Wu, et al. (2015) that men are more altruistic than women in a range of economic games, in Sino-Tibetan societies with equal male and female migration (duolocal post-marital residence), or medium female migration (patrilocal post-marital residence), or high female migration (strongly patrilocal post-marital residence). That is, our results suggest that this sex bias in altruism may have been driven by the recent past of intergroup conflict (e.g. cattle raiding) in these societies. Our study does not, however, immediately illuminate Wu, et al.'s (2015) finding that both men and women are less cooperative in duolocal populations, which are characterised by low and equal levels of male and female dispersal. Our results instead show that higher levels of philopatry drive higher levels of altruism. As suggested by Wu, et al. (2015), the inverse relationship between dispersal and altruism they uncovered might be due to altruistic behaviours being more targeted at the extended family (household) than the larger social group (village) in these duolocal populations. In future, the present analysis could be expanded to consider how pattern of altruism vary when these two levels of social organisation are considered explicitly.

How do our results compare with those of other studies investigating sex differences in altruism? This question has generated considerable interest in the past few years, but a consensus has not yet been reached. A meta-analysis of experimental studies of mainly WEIRD subjects (Western, Educated, Industrialized, Rich, and Democratic; Henrich, et al., 2010) could not identify a difference in the extent of cooperativeness exhibited by males and females (Balliet, et al., 2011). However, the same study found that interactions between men are more cooperative than interactions between women, and that women are more cooperative in mixed sex interactions (Balliet, et al., 2011). A pattern that is reminiscent of this is obtained in our model when dispersal is female-biased and admixture is higher for men than for women (illustrated in panel f, Fig.4.1 and Fig4.2). Another meta-analysis finds instead that women give more than men in Dictator games and also receive more (Engel, 2011; in the context of the male warrior hypothesis, van Vugt, et al., 2006 also find that women are more cooperative, but men increase their cooperativeness when the group is under threat). This would be more in line with our results for male-biased dispersal and higher female than male admixture (illustrated in panel h, Fig.4.1 and Fig4.2).

Our aim has been to capture how sex-specific demography modulates sex-specific altruism in the context of human warfare. To this end, we have focused on the role of dispersal and admixture, whilst assuming that both sexes are equally capable of helping, in terms of them experiencing the same costs and providing the same benefits to their recipients. However, if the sexes did differ in the costs and benefits of altruism, then this –

fairly trivially – would be expected to drive sex differences in their altruistic behaviour. For example, if one sex were less effective in helping – i.e. providing a lower benefit – this would lead to a higher cost-to-benefit ratio and thus a lower level of altruism than for the more effective sex. If instead the two sexes were equally effective in helping, but one incurred lower costs associated with it, this would lead to a lower cost-to-benefit ratio and thus a higher level of altruism than for the sex experiencing more substantial costs.

Moreover, for simplicity, we have assumed that the effects of different altruistic behaviours on an individual's competitiveness for reproductive opportunities are multiplicative. In this way, levels of male-to-male, male-to-female, female-to-male and female-to-female altruism do not interfere with each other and could be considered to evolve independently. However, if the costs incurred by the altruist and/or the benefits provided to the recipients depended on the levels of altruism currently performed by other individuals, patterns of altruism could differ from the ones obtained in the present analysis. Specifically, there is the potential for evolutionary feedbacks between different altruistic behaviours (analogous to the feedbacks between male and female participation in warfare uncovered in Micheletti, et al., 2018; Chapter 3). Exploration of such interactions between altruistic behaviours and coevolutionary feedbacks is a promising avenue for future investigation of the links between warfare and altruism.

Extended Methods

Preamble

Here, we adapt an existing model of warfare (Lehmann and Feldman, 2008; Micheletti, et al., 2017, 2018; Chapters 2 and 3) to investigate the evolution of sex-specific altruism – i.e.

a behaviour that results in a decrease in competitiveness for the altruist and an increase in competitiveness for the recipient (Hamilton, 1964; West, et al., 2007) – in the context of the demography of war. We adopt the life cycle described in these three studies, but we consider the probability that a group attacks another one and the probability that the attacking group wins the war as non-evolving parameters. We consider four altruistic traits: male-to-female altruism, female-to-male altruism (see *Altruism to opposite sex – marginal fitness*), male-to-male altruism, female-to-female altruism (see *Altruism to same sex – marginal fitness*).

Fitness

We first derive the absolute fitness of a focal young adult individual of sex $i \in \{m,f\}$ (see life cycle in Methods). With probability $1 - m_i$, the focal young adult of sex-i does not disperse from the focal group. In every generation, each post-dispersal group can attack one randomly-chosen group. With probability $1 - a$, the focal group is not attacked by the other group. In this case the focal sex-i young adult competes for N_i breeding spots with $N_f K_i$ sex i young adults, where N_f is adult females (notice that a fraction $1 - m_i$ of these sex i young adults originated from the focal group, while the remaining proportion m_i migrated from another group; the dispersal terms cancel out). The focal sex i young adult has competitiveness for reproductive spots t_i and his groupmates t_i'. Therefore, the probability that a focal sex i young adult secures a breeding spot is $(N_i t_i)/(N_f K_i t_i')$. Alternatively, with probability a, the focal group is attacked and the attacking group loses the war with probability $1 - \omega$, in which case the probability that a focal sex i young adult secures a breeding spot is again $(t_i N_i)/(t_i' N_f K_i)$. Otherwise, the attacking group wins the war with probability ω, in which case it the focal sex-i young adult competes for $N_i(1 - \sigma_i)$ breeding spots with $N_f K_i(1 - \sigma_i)$ sex-i young adults from their group and $N_f K_i \sigma_i$ sex-i young adults from the attacking group – resulting in a probability $N_i(1 - \sigma_i)t_i/(N_f K_i(1 - \sigma_i)t_i' + N_f K_i \sigma_i \bar{t}_i)$ that the focal sex i young adult obtains a reproductive spot. In addition, the focal group may attack one other group. With probability $1 - a$, this does not happen, and with probability $a(1 - \omega)$, they attack but lose the war: in either case, the focal sex-i young adult does not have access to additional reproductive spots. If instead the focal group attacks another group and wins the war – which occurs with probability $a\omega$, then the focal sex-i young adult has access to an additional $N_i\sigma_i$ breeding spots, for which he competes with $N_fK_i\sigma_i$ sex-i young adults from their group and $N_fK_i(1 - \sigma_i)$ sex-i young adults from the conquered group – resulting in a probability $N_i\sigma_i t_i/(N_f K_i\sigma_i t_i' + N_f K_i(1 - \sigma_i)\ \bar{t}_i)$ that the focal sex i young adult obtains a breeding spot. Alternatively, the focal sex-i young adult disperses from the natal group with probability m_i to a randomly chosen group. In this case, the probabilities that a focal individual of sex i obtains a reproductive spot are identical to the case described above in which they do not disperse. Notice that the dispersal terms cancel out and thus do not appear in the fitness function (but dispersal has an impact on relatedness, see *Consanguinity and relatedness*). Therefore, the fitness of a focal sex-i young adult is given by:

$$w_\mathrm{i} = \left((1-a)\frac{t_\mathrm{i}}{t_\mathrm{i}'} + a\left((1-\omega)\frac{t_\mathrm{i}}{t_\mathrm{i}'} + \omega\frac{(1-\sigma_\mathrm{i})t_\mathrm{i}}{(1-\sigma_\mathrm{i})t_\mathrm{i}' + \sigma_\mathrm{i}\bar{t}_\mathrm{i}} \right) + a\omega\frac{\sigma_\mathrm{i} t_\mathrm{m}}{\sigma_\mathrm{i} t_\mathrm{i}' + (1-\sigma_\mathrm{i})\bar{t}_\mathrm{i}} \right)\frac{N_\mathrm{i}}{N_\mathrm{f}K_\mathrm{i}} \qquad [A4.1]$$

The average fitness of a sex-i young adult in the population is obtained by setting $t_i = t_i' = \bar{t}_i$ and is given by $\bar{w}_i = N_i/(N_fK_i)$. The relative fitness of the focal sex-i young adult is given by $W_i = w_i / \bar{w}_i$. The relative fitness of a young adult of unspecified sex in a focal group in a sex-structured population is a weighted average of the relative fitness of male and female individuals and is given by $W = c_m W_m + c_f W_f$, where c_m and c_f are the class reproductive values for males and females, respectively (Fisher 1930, Price & Smith 1972, Taylor & Frank 1996, Frank 1997, Taylor et al 2007).

Altruism to opposite sex – marginal fitness

Consider a locus G, which controls altruism performed by individuals of sex i ∈{m,f} towards individuals of the opposite sex, j, and denoted by x_{ij}. This trait is expressed only by young adults of sex i, but impacts the competitiveness for breeding spots of individuals both sex i and sex j in their group. Let g be the genic value of the focal young adult for this gene, G the breeding value of the focal young adult, G' the breeding value of a randomly-chosen groupmate of the focal young adult, and $\bar{G}$ the average of the population.

Assuming vanishing genetic variation – all breeding values clustered around the mean (Taylor and Frank, 1996; Frank, 1997) – the direction of natural selection is given by:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_{\mathrm{i}}\frac{\mathrm{d}W_{\mathrm{i}}}{\mathrm{d}g_{\mathrm{i}}} + c_{\mathrm{j}}\frac{\mathrm{d}W_{\mathrm{j}}}{\mathrm{d}g_{\mathrm{j}}}, \qquad \text{[A4.2]}$$

with all derivatives evaluated at $g = g_{\mathrm{i}} = g_{\mathrm{j}} = \bar{G}$.

The first derivative in equation [A4.2] describes the impact of the genic value of a gene drawn from a sex-i young adult on their relative fitness. This can be expanded, employing the chain rule, obtaining:

$$\frac{\mathrm{d}W_{\mathrm{i}}}{\mathrm{d}g_{\mathrm{i}}} = \frac{\partial W_{\mathrm{i}}}{\partial x_{\mathrm{ij}}}\frac{\mathrm{d}x_{\mathrm{ij}}}{\mathrm{d}G}\frac{\mathrm{d}G}{\mathrm{d}g_{\mathrm{i}}} + \frac{\partial W_{\mathrm{i}}}{\partial x_{\mathrm{ij}'}}\frac{\mathrm{d}x_{\mathrm{ij}'}}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_{\mathrm{i}}} = \left(\frac{\partial W_{\mathrm{i}}}{\partial x_{\mathrm{ij}}}p_{\mathrm{self}} + \frac{\partial W_{\mathrm{i}}}{\partial x_{\mathrm{ij}'}{}'}p_{\mathrm{ii}}\right)\gamma, \qquad \text{[A4.3]}$$

where $\mathrm{d}W_{\mathrm{i}}/\mathrm{d}x_{\mathrm{ij}}$ is the impact of the altruistic behaviour performed by the focal sex-i young adult on their fitness, $\mathrm{d}W_{\mathrm{i}}/\mathrm{d}x_{\mathrm{ij}}'$ is the impact of the altruistic behaviour performed by a random sex-i young adult in the focal group on the fitness of the focal sex-i young adult, $p_{\mathrm{self}} = \mathrm{d}G/\mathrm{d}g_{\mathrm{i}}$ is the consanguinity of the focal sex-i young adult to themselves, $p_{\mathrm{ii}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{i}}$ is the consanguinity between the focal sex-i young adult and a random sex-i young adult in their group, and $\gamma = \mathrm{d}x_{\mathrm{ij}}/\mathrm{d}G = \mathrm{d}x_{\mathrm{ij}}'/\mathrm{d}G'$ is the correlation between a young adult's phenotype and their breeding value.

The second derivative in equation [A4.2] describes the impact of the genic value of a gene drawn from a young adult of the other sex (sex j) on their relative fitness. Expanding it, employing the chain rule, reveals an indirect fitness component (no direct fitness component as sex-j young adults do not perform the behaviour). In mathematical form:

$$\frac{\mathrm{d}W_{\mathrm{j}}}{\mathrm{d}g_{\mathrm{j}}} = \frac{\partial W_{\mathrm{j}}}{\partial x_{\mathrm{ij}'}}\frac{\mathrm{d}x_{\mathrm{ij}'}}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_{\mathrm{j}}} = \frac{\partial W_{\mathrm{j}}}{\partial x_{\mathrm{ij}'}}p_{\mathrm{ij}}\,\gamma, \qquad \text{[A4.4]}$$

where $\mathrm{d}W_{\mathrm{j}}/\mathrm{d}x_{\mathrm{ij}}'$ is the impact of the altruistic behaviour performed by a random sex-i young adult in the focal group on the fitness of the focal sex-j young adult, $p_{\mathrm{ij}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{j}}$ is the consanguinity between the focal sex-j young adult and a random sex-i young adult in their group, and $\gamma = \mathrm{d}x_{ij}'/\mathrm{d}G'$ is again the correlation between a young adult's phenotype and their breeding value.

Altruism performed by sex i towards sex j has an impact on both sex-i competitiveness for breeding positions t_i and sex-j competitiveness t_j (see Methods). Therefore: $\partial W_i/\partial x_{ij} = (\partial W_i/\partial t_i)(\partial t_i/\partial x_{ij})$, $\partial W_i/\partial x_{ij}' = (\partial W_i/\partial t_i')(\partial t_i'/\partial x_{ij}')$, $\partial W_j/\partial x_{ij}' = (\partial W_j/\partial t_j)(\partial t_j/\partial x_{ij}') + (\partial W_j/\partial t_j')(\partial t_j'/\partial x_{ij}')$, where $t_i=T_i(x_{ij})$, $t_i'=T_i(x_{ij}')$, $\bar{t}_i=T_i(\bar{x}_{ij})$, $t_j=t_j'=T_j(x_{ij}')$, $\bar{t}_j=T_j(\bar{x}_{ij})$ and where $\partial T_i(x_{ij})/\partial x_{ij} = \partial T_i(x_{ij}')/\partial x_{ij}' = -\bar{t}_i \mathrm{c}_{ij}$ and $\partial T_j(x_{ij}')/\partial x_{ij}' = +\bar{t}_i \mathrm{b}_{ij}$. Substituting these expressions and equations [A3.2] and [A3.3] into equation [A3.1] we obtain:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_\mathrm{i}\left(\frac{\partial W_\mathrm{i}}{\partial t_\mathrm{i}}(-c_\mathrm{ij}\bar{t}_\mathrm{i})p_\mathrm{self} + \frac{\partial W_\mathrm{i}}{\partial t_{\mathrm{i}'}}(-c_\mathrm{ij}\bar{t}_\mathrm{i})p_\mathrm{ii}\right)\gamma \ + c_\mathrm{j}\left(\frac{\partial W_\mathrm{i}}{\partial t_\mathrm{j}}b_\mathrm{ij}\bar{t}_\mathrm{j} + \frac{\partial W_\mathrm{i}}{\partial t_{\mathrm{i}'}}b_\mathrm{ij}\bar{t}_\mathrm{j}\right) p_\mathrm{ij}\,\gamma \qquad [A4.5]$$

Population average altruism by sex i towards sex j increases when dW/dg > 0. Substituting the appropriate derivatives in equation [A4.5], this condition is given by

$$c_\mathrm{i}\left(-c_\mathrm{ij}p_\mathrm{self} + \alpha_\mathrm{i}c_\mathrm{ij}p_\mathrm{ii}\right)\gamma \ + c_\mathrm{j}\left(b_\mathrm{ij} - \alpha_\mathrm{i}b_\mathrm{ij}\right) p_\mathrm{ij}\,\gamma > 0 \qquad [A4.6]$$

If $c_i = c_j = ½$ (as is the case under diploid inheritance, i.e. the case considered here), this simplifies to:

$$-c_\mathrm{ij}p_\mathrm{self} + \alpha_\mathrm{i}c_\mathrm{ij}p_\mathrm{ii} + \left(b_\mathrm{ij} - \alpha_\mathrm{i}b_\mathrm{ij}\right) p_\mathrm{ij} > 0 \qquad [A4.7]$$

Dividing by p_self to obtain relatedness coefficients ($r_{ii} = p_{ii}/p_\mathrm{self}$ and $r_{ij} = p_{ij}/p_\mathrm{self}$; see *Consanguinity and relatedness*) and rearranging terms yields

$$-c_\mathrm{ij} + \alpha_\mathrm{i}c_\mathrm{ij}r_\mathrm{ii} + \left(b_\mathrm{ij} - \alpha_\mathrm{i}b_\mathrm{ij}\right) r_\mathrm{ij} > 0 \qquad [A4.8]$$

which is condition [4.1] in Results.

Altruism to same sex – marginal fitness

Consider now that the locus G controls altruism performed by individuals of sex i $\in$ {m,f} towards individuals of the same sex – denoted by x_{ii}. This trait is expressed only by young adults of sex i and only impacts the competitiveness for breeding spots of individuals of sex i. Let g be the genic value of the focal young adult for this gene, G the breeding value of the focal young adult, G' the breeding value of a randomly-chosen groupmate of the focal young adult, and $\bar{G}$ the average of the population.

Assuming vanishing genetic variation – all breeding values clustered around the mean (Taylor and Frank, 1996; Frank, 1997) – the direction of natural selection is given by:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_{\mathrm{i}}\frac{\mathrm{d}W_{\mathrm{i}}}{\mathrm{d}g_{\mathrm{i}}} + c_{\mathrm{j}}\frac{\mathrm{d}W_{\mathrm{j}}}{\mathrm{d}g_{\mathrm{j}}}, \qquad \text{[A4.9]}$$

with all derivatives evaluated at $g = g_{\mathrm{i}} = g_{\mathrm{j}} = \bar{G}$.

The first derivative in equation [A4.9] describes the impact of the genic value of a gene drawn from a sex-i young adult on their relative fitness. This can be expanded, employing the chain rule, obtaining:

$$\frac{\mathrm{d}W_{\mathrm{i}}}{\mathrm{d}g_{\mathrm{i}}} = \frac{\partial W_{\mathrm{i}}}{\partial x_{\mathrm{ii}}}\frac{\mathrm{d}x_{\mathrm{ii}}}{\mathrm{d}G}\frac{\mathrm{d}G}{\mathrm{d}g_{\mathrm{i}}} + \frac{\partial W_{\mathrm{i}}}{\partial x_{\mathrm{ii}'}}\frac{\mathrm{d}x_{\mathrm{ii}'}}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_{\mathrm{i}}} = \left(\frac{\partial W_{\mathrm{i}}}{\partial x_{\mathrm{ii}}}p_{\mathrm{self}} + \frac{\partial W_{\mathrm{i}}}{\partial x_{\mathrm{ii}'}}p_{\mathrm{ii}}\right)\gamma, \qquad \text{[A4.10]}$$

where $\mathrm{d}W_{\mathrm{i}}/\mathrm{d}x_{\mathrm{ii}}$ is the impact of the altruistic behaviour performed by the focal sex-i young adult on their fitness, $\mathrm{d}W_{\mathrm{i}}/\mathrm{d}x_{\mathrm{ii}}'$ is the impact of the altruistic behaviour performed by a random sex-i young adult in the focal group on the fitness of the focal sex-i young adult, $p_{\mathrm{self}} = \mathrm{d}G/\mathrm{d}g_{\mathrm{i}}$ is the consanguinity of the focal sex-i young adult to themselves, $p_{\mathrm{ii}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{i}}$ is the consanguinity between the focal sex-i young adult and a random sex i young adult in their group, and $\gamma = \mathrm{d}x_{\mathrm{ii}}/\mathrm{d}G = \mathrm{d}x_{\mathrm{ii}}'/\mathrm{d}G'$ is the correlation between a young adult's phenotype and their breeding value.

The second derivative in equation [A4.9] describes the impact of the genic value of a gene drawn from a young adult of the other sex (sex j) on their relative fitness.

Considered that the trait under consideration is only expressed by individuals of sex i and is aimed only at individuals of sex i, this derivative is null.

Altruism performed by individuals of sex i towards groupmates of sex i has an impact only on sex-i competitiveness for breeding positions t_i (see Methods). Therefore: $\partial W_\mathrm{i}/\partial x_\mathrm{ii} = (\partial W_\mathrm{i}/\partial t_\mathrm{i})(\partial t_\mathrm{i}/\partial x_\mathrm{ij})$, $\partial W_\mathrm{i}/\partial x_\mathrm{ij}' = (\partial W_\mathrm{i}/\partial t_\mathrm{i})(\partial t_\mathrm{i}/\partial x_\mathrm{ij}') + (\partial W_\mathrm{i}/\partial t_\mathrm{i}')(\partial t_\mathrm{i}'/\partial x_\mathrm{ij}')$, with $t_\mathrm{i} = T_\mathrm{i}(y,z)$ where $y=x_\mathrm{ii}$ and $z=x_\mathrm{ii}'$, and with $t_\mathrm{i}' = T_\mathrm{i}(y,z)$ where $y=x_\mathrm{ii}'$ and $z=x_\mathrm{ii}'$. We define: $\partial t_\mathrm{i}/\partial y = \partial t_\mathrm{i}'/\partial y = -\bar{t}_\mathrm{i}\,\mathrm{c}_\mathrm{ii}$ and $\partial t_\mathrm{i}/\partial z = \partial t_\mathrm{i}'/\partial z = \bar{t}_\mathrm{i}\,\mathrm{b}_\mathrm{ii}$. Therefore we obtain: $\partial W_\mathrm{i}/\partial x_\mathrm{ii} = (\partial W_\mathrm{i}/\partial t_\mathrm{i})(-\bar{t}_\mathrm{i}\,\mathrm{c}_\mathrm{ii})$ and $\partial W_\mathrm{i}/\partial x_\mathrm{ij}' = (\partial W_\mathrm{i}/\partial t_\mathrm{i})(\bar{t}_\mathrm{i}\,\mathrm{b}_\mathrm{ii}) + (\partial W_\mathrm{i}/\partial t_\mathrm{i}')(-\bar{t}_\mathrm{i}\,\mathrm{c}_\mathrm{ii} + \bar{t}_\mathrm{i}\,\mathrm{b}_\mathrm{ii})$. Substituting these expressions and equation [A4.2] into equation [A4.1] we obtain:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_\mathrm{i}\left(\frac{\partial W_\mathrm{i}}{\partial t_\mathrm{i}}(-c_\mathrm{ii}\bar{t}_\mathrm{i})p_\mathrm{self} + \left(\frac{\partial W_\mathrm{i}}{\partial t_\mathrm{i}}b_\mathrm{ii}\bar{t}_\mathrm{i} + \frac{\partial W_\mathrm{i}}{\partial t_\mathrm{i}'}(-c_\mathrm{ii}\bar{t}_\mathrm{i} + b_\mathrm{ii}\bar{t}_\mathrm{i})\right)p_\mathrm{ii}\right)\gamma \qquad \text{[A4.11]}$$

Population average altruism by sex i towards the same sex increases when $\mathrm{d}W/\mathrm{d}g > 0$. Substituting the appropriate derivatives in equation [A4.11], this condition is given by:

$$c_\mathrm{i}(-c_\mathrm{ii}p_\mathrm{self} + (b_\mathrm{ii} + (\alpha_\mathrm{i}c_\mathrm{ii} - \alpha_\mathrm{i}b_\mathrm{ii}))p_\mathrm{ii})\gamma > 0 \qquad \text{[A4.12]}$$

If $c_\mathrm{i} = c_\mathrm{j} = ½$ (as is the case under diploid inheritance, i.e. the case considered here), this simplifies to:

$$-c_\mathrm{ii}p_\mathrm{self} + (b_\mathrm{ii} + (\alpha_\mathrm{i}c_\mathrm{ii} - \alpha_\mathrm{i}b_\mathrm{ii}))p_\mathrm{ii} > 0 \qquad \text{[A4.13]}$$

Dividing by p_self to obtain relatedness coefficients ($r_\mathrm{ii} = p_\mathrm{ii}/p_\mathrm{self}$ and $r_\mathrm{ij} = p_\mathrm{ij}/p_\mathrm{self}$; see *Consanguinity and relatedness*) and rearranging terms, we obtain:

$$-c_\mathrm{ii} + \alpha_\mathrm{i}c_\mathrm{ii}r_\mathrm{ii} + (b_\mathrm{ii} - \alpha_\mathrm{i}b_\mathrm{ii})\,p_\mathrm{ii} > 0 \qquad \text{[A4.14]}$$

which is condition [4.2] in Results. Notice that this condition can be obtained from condition [A4.8] (the condition for increase for altruism by sex i towards sex j) by setting j=i. This is coincidental and is due to the two sexes having the same class reproductive values under diploidy.

A derivation of a general case – altruism by sex i $\in$ {m,f} towards sex j $\in$ {m,f}, where i=j is allowed – was attempted, but without success. This confirms that altruism towards same-sex groupmates and altruism towards opposite-sex groupmates are not the same behaviour. This can be seen by comparing conditions [A4.6] and [A4.12] (i.e. the step in the derivation right before the numerical values of the class reproductive values are substituted in the condition for increase).

Consanguinity and relatedness

The consanguinity coefficient between two individuals A and B at a given locus, p_{AB}, is defined as the probability that a gene randomly-drawn from individual A at that locus is identical-by-descent to a gene randomly-drawn from individual B at that same locus (Bulmer, 1994).

The consanguinity of an individual to themselves (i.e. the case in which B=A) is given by $p_{\mathrm{self}} = (1 + f)/2$. The consanguinity between adult mating partners in a post-competition group is known as 'inbreeding coefficient' and is given by $f = \varphi_{\mathrm{mf}}\, p_{\mathrm{x}}$. Similarly, the consanguinity between two sex-i adults (with i $\in$ {m,f}) in a post-dispersal group is given by $p_{\mathrm{ii,adult}} = \varphi_{\mathrm{ii}}\, p_{\mathrm{x}}$. The probabilities that two adults of opposite sex and two adults of sex i, who are in the same post-competition group, were born in the same group, are given by, $\varphi_{\mathrm{mf}} = (1 - \bar{a}\ \bar{\omega}\ (2(1 - \sigma_{\mathrm{m}})(1 - \sigma_{\mathrm{f}}) - (1 - \sigma_{\mathrm{m}}) - (1 - \sigma_{\mathrm{f}}))(1 - m_{\mathrm{m}})(1 - m_{\mathrm{f}})$ and $\varphi_{\mathrm{ii}} = (1 - 2\ \bar{a}\ \bar{\omega}\ \sigma_{\mathrm{i}}(1 - \sigma_{\mathrm{i}}))(1 - m_{\mathrm{i}})^2$, respectively. The consanguinity of individuals born in the same group, p_{x}, is given by:

$$p_{\mathrm{x}} = \frac{1}{4}\left(\frac{1}{N_{\mathrm{m}}} p_{\mathrm{self}} + \frac{N_{\mathrm{m}}-1}{N_{\mathrm{m}}} p_{\mathrm{mm,adult}}\right) + \frac{1}{2} f + \frac{1}{4}\left(\frac{1}{N_{\mathrm{f}}} p_{\mathrm{self}} + \frac{N_{\mathrm{f}}-1}{N_{\mathrm{f}}} p_{\mathrm{ff,adult}}\right) \qquad \text{[A4.15]}$$

Substituting in consanguinities and solving for p_{x}, we obtain:

$$p_{\mathrm{x}} = \frac{(N_{\mathrm{m}}+N_{\mathrm{f}})\ \varphi_{\mathrm{mf}}}{8\ N_{\mathrm{m}}\ N_{\mathrm{f}} - 2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\ \varphi_{\mathrm{mm}} - 2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\ \varphi_{\mathrm{ff}} - (4N_{\mathrm{m}}\ N_{\mathrm{f}} + N_{\mathrm{m}} + N_{\mathrm{f}})\varphi_{\mathrm{mf}}}. \qquad \text{[A4.16]}$$

In a post-dispersal group, the consanguinity of a focal sex-i young adult to a random sex-i young adult is equal to the probability that the two sex-i young adults were born in the same group and that both remained in it (i.e. neither dispersed), that is $p_{ii} = (1 - m_i)^2 p_x$. Analogously, the consanguinity of a focal sex-i young adult to a random sex-j young adult is equal to the probability that the sex-i and the sex-j young adults were born in the same group and that both reimained in it (i.e. neither dispersed), that is $p_{ij} = (1 - m_i)(1 - m_j) p_x$.

The relatedness coefficient between two individuals A and B at a given locus, r_{AB}, is obtained by dividing p_{AB} by $p_{BB} = p_{self}$ (Bulmer, 1994). The relatedness between two individuals born in the same group is given by $r_x = p_x/p_{self}$, the relatedness between two sex-i young adults in a post-dispersal group is given by $r_{ii} = p_{ii}/p_{self} = (1 - m_i)^2 r_x$, and the relatedness between a sex-i young adult and a sex-j young adult in a post-dispersal group is given by $r_{ij} = p_{ij}/p_{self} = (1 - m_i)(1 - m_j) r_x$.

Demonstrations

Here, we demonstrate how sex biases in dispersal and admixture impact on pattern of sex-specific altruism. The potential for altruism towards the same sex is given by $A_{ii} = (r_{ii} - \alpha_i r_{ii})/(1 - \alpha_i r_{ii})$ whereas the potential for altruism towards the opposite sex is given by $A_{ij} = (r_{ij} - \alpha_j r_{ij})/(1 - \alpha_i r_{ii})$.

First, we demonstrate that, assuming $M_i = M_j$, if $m_i < m_j$ then $A_{ii} > A_{ij}$; that is, all else being equal, the more philopatric sex has a higher potential for altruism towards the same sex than the opposite sex. Assuming $M_i = M_j$, it follows that $\alpha_i = \alpha_j = \alpha$ and thus the potentials are $A_{ii} = (r_{ii} - \alpha r_{ii})/(1 - \alpha r_{ii})$ and $A_{ij} = (r_{ij} - \alpha r_{ij})/(1 - \alpha r_{ii})$.If $m_i < m_j$, then $r_{ii} > r_{ij}$ (see *Consanguinity and relatedness*) and therefore $A_{ii} > A_{ij}$.

Second, we demonstrate that, assuming $m_i = m_j$, if $M_i > M_j$ then $A_{ii} > A_{ij}$; that is, all else being equal, the sex that is characterised by a higher degree of admixture has a higher potential for altruism towards the same sex than the opposite sex. Assuming $m_i = m_j$, it follows $r_{ii} = r_{ij} = r$ (see *Consanguinity and relatedness*) and thus the potentials are $A_{ii} = (r - \alpha_i r)/(1 - \alpha_i r)$ and $A_{ij} = (r - \alpha_j r)/(1 - \alpha_i r)$. If $M_i > M_j$, then $\alpha_i < \alpha_j$ and therefore $A_{ii} > A_{ij}$.

Third, we demonstrate that, assuming $M_i > M_j$ and $m_i < m_j$, then it is always true that $A_{ii} > A_{ij}$; that is, the sex that is characterised by higher admixture and is more philopatric always has a higher potential for altruism towards the same sex than the opposite sex. Assuming $M_i > M_j$, it follows that $\alpha_i < \alpha_j$ and assuming $m_i < m_j$ it follows that $r_{ii} > r_{ij}$. Therefore $(1 - \alpha_i)r_{ii} > (1 - \alpha_j)r_{ij}$, which implies $A_{ii} > A_{ij}$.

Fourth, we demonstrate that, assuming $M_i > M_j$ and $m_i > m_j$, then it is $A_{ii} > A_{ij}$ or $A_{ii} < A_{ij}$ depending on values of M_i, M_j, m_i, m_j; that is, the sex that is characterised by higher admixture and a higher rate of dispersal may have a higher potential for altruism towards the same sex or the opposite sex, depending on parameter values. Assuming $M_i > M_j$, it follows that $\alpha_i < \alpha_j$ and assuming $m_i > m_j$ it follows that $r_{ii} < r_{ij}$. Therefore it may be $(1 - \alpha_i)r_{ii} > (1 - \alpha_j)r_{ij}$ (which implies $A_{ii} > A_{ij}$) or it may be $(1 - \alpha_i)r_{ii} < (1 - \alpha_j)r_{ij}$ (which implies $A_{ii} < A_{ij}$).

Illustrations

For the purposes of illustrating predicted convergence-stable levels of altruism (Fig. 4.2), we make the competitiveness function explicit. For simplicity, we assume competitiveness functional form $t_{i,ind} = (1 - \chi\, x_{ii,ind})\,(1 - \chi\, x_{ij,ind})\, x_{ii,grp}\, x_{ji,grp}$ in which the effects of i-to-i, i-to-j and j-to-i altruism are multiplicative. In this way the four traits under consideration do not influence each other and they can be considered to evolve independently.

5 Conflicts within and between groups inhibit alliance formation in human warfare and the evolution of larger-scale human societies

> If an enemy has alliances, the problem is grave and the enemy's position strong; if he has no alliances, the problem is minor and the enemy's position weak.
>
> –Sun Tzu, *The Art of War*
> (trans. S. B. Griffith)

> There is no theoretical reason to expect evolutionary lineages to increase in complexity with time, and no empirical evidence that they do.
>
> –Eörs Szathmáry & John Maynard Smith (1995)

Abstract

The evolution of human societies from smaller foraging groups to larger-scale states with multiple organisational levels represents one of the most striking facets of our species' history, and understanding the drivers of this major transition remains an enduring challenge for researchers across multiple disciplines. Warfare is often argued to have played a key role in welding small human groups together to form larger alliances that are able to field more combatants and thus win more confrontations. This suggestion has given rise to the view that war-stricken regions are cradles of civilization. However, whilst these arguments have focused on potential benefits to the nascent alliance as a whole, the wider study of major evolutionary transitions – including the evolution of the eukaryotic cell, multicellularity and eusociality – has repeatedly shown that conflicts of interest at lower levels are often crucial in determining whether and how new higher-level entities emerge. Here, we develop mathematical models of alliance formation via conquest to assess the scope for – and consequences of – conflicts of interest between and within human groups. We reveal that between-group conflict will often arise over the reproductive concessions that defeated parties must make to their conquerors. Moreover, we show that negotiation of alliances will often present collective-action problems that manifest as within-group conflicts – such that the likelihood of alliance formation need not be greater in more bellicose populations. Taken together, these results suggest that conflicts of interest may inhibit the emergence of larger-scale multi-group societies, unless they are counteracted by mechanisms ensuring suppression of within-group competition.

Introduction

In the past 13,000 years, our societies have increased in size, with human groups associating in various ways to form higher-level polities: single bands have – in some cases – joined together to form multi-community tribes, and these have then transitioned – again, not universally – into stratified chiefdoms, some of which have later developed into states, characterised by more than two levels of organisation (Currie, et al., 2010; Turchin, 2010). In recent years, this process has attracted a great deal of multi-disciplinary attention, from archaeology and anthropology, to psychology and evolutionary biology (Diamond, 1997;

Currie, et al., 2010; Turchin, 2010, 2015; Turchin, et al., 2013; Spencer, 2010; Gat, 2006; Morris, 2014; Turchin and Gavrilets, 2009; Gavrilets, et al., 2010) and it has been identified as one of a small number of 'major transitions' that have occurred throughout the history of life on Earth (Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1995; Stearns, 2007; Turchin, 2010). The major transitions in individuality entail previously independent entities forming a higher-level unit by becoming interdependent, and include the shift from molecular replicators to cellular life, from individual cells to multicellular organisms, and from individual organisms to eusocial colonies (Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1995).

Major transitions are understood to be driven by fundamental benefits arising from synergistic fitness interactions, division of labour, and economies of scale; meaning that a higher-level unit is able to exploit resources more efficiently than can its constituent subunits on their own (Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1995; Queller, 1997; Bourke, 2011; Szathmary, 2015; West, et al, 2015). Exploration of such benefits in increasingly large and hierarchically-structured human groups has been at the centre of anthropological and sociological theories of socio-political evolution in the past century (Service, 1962, 1975; Carneiro, 1970, 1998, 2003; Flannery, 1972; Wright, 1977, 2006; Spencer, 1990, 2010; Sanderson, 1999; Johnson and Earle, 2000). In this context, warfare has been repeatedly suggested as the pivotal factor in the evolution of larger-scale multi-group societies: in particular, the tendency for military success to be disproportionately greater for the side with more combatants has been argued to result in groups forming cooperative associations with each other, for example through military alliances (Carneiro 1970, 1998, 2003; Wright 1977, 2006; Spencer, 1990, 2010].

Recent work has helped to further advance the rationale for this idea, drawing from particular examples throughout recorded history (Gat, 2006; Morris, 2014; Turchin, 2015), and developing mathematical and simulation models of polity evolution, which suggest that a higher intensity of war results in political formations that are both larger and more hierarchically-structured (i.e. groups-of-groups; Turchin and Gavrilets, 2009; Gavrilets, et al., 2010; Turchin, 2010; Turchin, et al., 2013).

However, whilst the group-level benefits of large size are essentially ubiquitous, major transitions to higher-level entities are by no means inevitable, as they are often opposed by conflicts of interest between lower-level units with contrasting evolutionary agendas (Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1995; Queller, 1997; Bourke, 2011; Fisher, et al, 2013; Szathmary, 2015; West, et al., 2015). Accordingly, explaining why certain taxa have undergone major transitions while others have not requires careful scrutiny of these lower-level conflicts and the ways in which they can be resolved (Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1995; Queller, 1997; Bourke, 2011; Fisher, et al, 2013; Szathmary, 2015; West, et al., 2015). In the case of alliance formation between human groups, the benefits of greater military strength will often be counterbalanced by a range of costs – and these need not be experienced evenly by all participants in the alliance, thus generating conflicts of interest. For example, a conquering group that enters into an alliance with a group they have defeated might do so at the cost of extracting fewer reproductive resources from them than would be taken in the absence of alliance formation, whereas the defeated group might suffer costs from forming the alliance associated with having to join their conquerors in unwanted future war campaigns. Moreover, whilst alliance-formation decisions have usually been studied from the perspective of what is best for the group, (Turchin and Gavrilets, 2009; Gavrilets, et al, 2010; Turchin, 2010), these will often represent collective-action problems that may ignite conflicts of interest within pre-existing social groups. Yet, the consequences of such within-group conflict remains to be investigated.

Here, we provide a mathematical assessment of the costs and benefits associated with alliance formation in the context of human warfare, allowing us to explore conflicts of interest between and within groups and determining their impact upon the likelihood of an alliance emerging. We extend an existing mathematical model of human warfare (Lehmnan and Feldman, 2008; Micheletti, et al., 2017, 2018; Chapter 2 and 3) by incorporating the possibility of alliances arising between conquering and defeated groups, and perform two complementary analyses to assess: a) potential conflicts of interest between a conquering group and a defeated group, and their ecological drivers; b) potential outcomes of such conflicts on the likelihood of alliance formation, with the exploration of potential collective action problems in the conquering groups and with implications for the nature and stability of military associations between groups.

Methods

We consider a large population organised into small-scale groups with sex-specific rates of migration, m_{m} and m_{f}. Groups attack and are attacked by other groups, with frequency a. If the attacking group defeats the defending group, an alliance between the two may be formed. In the event of no alliance being formed, a proportion σ_{m} and σ_{f} of the defeated group's male and female reproductive opportunities, respectively, are taken by individuals of the conquering group. In contrast, if an alliance is formed, the defeated group cedes proportions $\tau_\mathrm{m} \leq \sigma_\mathrm{m}$ and $\tau_\mathrm{f} \leq \sigma_\mathrm{f}$ of male and female reproductive opportunities, respectively, to individuals of the conquering group – we term this the 'tribute' made by the defeated group to their conquerors. In addition, by accepting allegiance, the defeated group is compelled to defend their ally should the latter be subsequently attacked by another group, which incurs a loss of competitiveness κ for all members of the defeated group – which we term 'fatigue' – but increases their ally's probability of repelling their attacker by Δ (see Extended Methods for details).

Results

First, we explore the interests of a conquering group, by hypothetically granting full control over alliance formation to its members and seeing whether or not they favour the alliance (Godfray, 1991, 1995). We find that the conquering group favours the formation of an alliance with a group they have attacked and defeated when:

$$-S + T + B_\mathrm{conq}\, S > 0 \qquad [5.1]$$

where $S = \sigma_\mathrm{m} + \sigma_\mathrm{f}\, v$ represents the weighted sum of male and female reproductive opportunities seized by the conquerors from the defeated group when an alliance is not formed, v is the relative value of female versus male reproductive success, $T = \tau_\mathrm{m} + \tau_\mathrm{f}\, v$ is the overall tribute ceded by the defeated group to the conquerors when an alliance is formed, and B_conq describes the benefits afforded by the alliance to the conquerors, owing to increased chances of winning a future defensive war and dependent on the frequency of war and the extent of ally fatigue (see Extended Methods for details). That is, by forming an alliance, a conquering group refrains from seizing some reproductive opportunities S from the defeated group thus incurring a fitness cost (first term in condition [5.1]), but obtains a tribute T amounting to a fitness benefit (second term) at the moment of alliance formation, and preserves reproductive opportunities S in their own group with probability B_{conq} (third term) in the context of a possible future war. Condition [5.1] can be rearranged as $T > S(1 - B_{\text{conq}})$, meaning that the conquering group favours an alliance only if the tribute is sufficiently *large*, i.e. greater than a minimum tolerated threshold level.

Considering next the interests of the defeated group, we find that they favour the formation of an alliance with their conquerors when:

$$S - T - C_{\text{def}}\, S > 0 \qquad [5.2]$$

where C_{def} describes the costs of alliance formation for the defeated group, owing to the possibility of being pulled into an additional war in aid of their ally and suffering a competitiveness disadvantage due to fatigue (see Extended Methods for details). That is, by forming an alliance, a defeated group preserves $S - T$ reproductive opportunities at alliance formation (first and second terms in condition [5.2]) thus obtaining an overall potential fitness benefit – as the reproductive opportunities ceded as tribute are equal or lower than those otherwise lost – but they also incur a fitness cost S with probability C_{def} (third term) as a result of committing to help their ally if the latter comes under attack. Condition [5.2] can be expressed as $T < S(1 - C_{\text{def}})$, meaning that the defeated group favours an alliance only if the tribute is sufficiently *small*, i.e. less than a maximum tolerated threshold level.

We have shown that the conditions under which a conquering and a defeated group favour an alliance are not the same and – for a given amount of tribute – the two groups might disagree as to whether to form such a military association. A given amount of tribute might be: unacceptable to both groups, in which case the two parties are not in conflict, as neither favours an alliance; acceptable to only one group, in which case the two parties are in conflict, with one favouring and the other disfavouring an alliance; acceptable to both groups, in which case their interests overlap, and they both favour an alliance. We find that whether the first, the second or the third scenario is realised is modulated by three factors in the ecology of war: the frequency of intergroup confrontations (a), the extent to which larger forces are more successful in battle (Δ), and the effect of fatigue on the allied group (κ; see Fig. 5.1). Note that ecological conditions exist under which no amount of tribute is acceptable to either group and thus military associations cannot be favoured by either party.

We find that, in contrast to previous suggestions, a higher frequency of war need not inevitably lead to a greater likelihood of alliance formation. With increasing probability of being attacked (a), the incentive for alliance from the perspective of the conquering group becomes stronger (i.e. their minimum tolerated tribute threshold decreases) because the benefits of having an ally become more substantial. However, the incentive for alliance from the perspective of the defeated group becomes weaker (i.e. their maximum tolerated tribute threshold decreases) owing to the higher likelihood of incurring the costs of fatigue

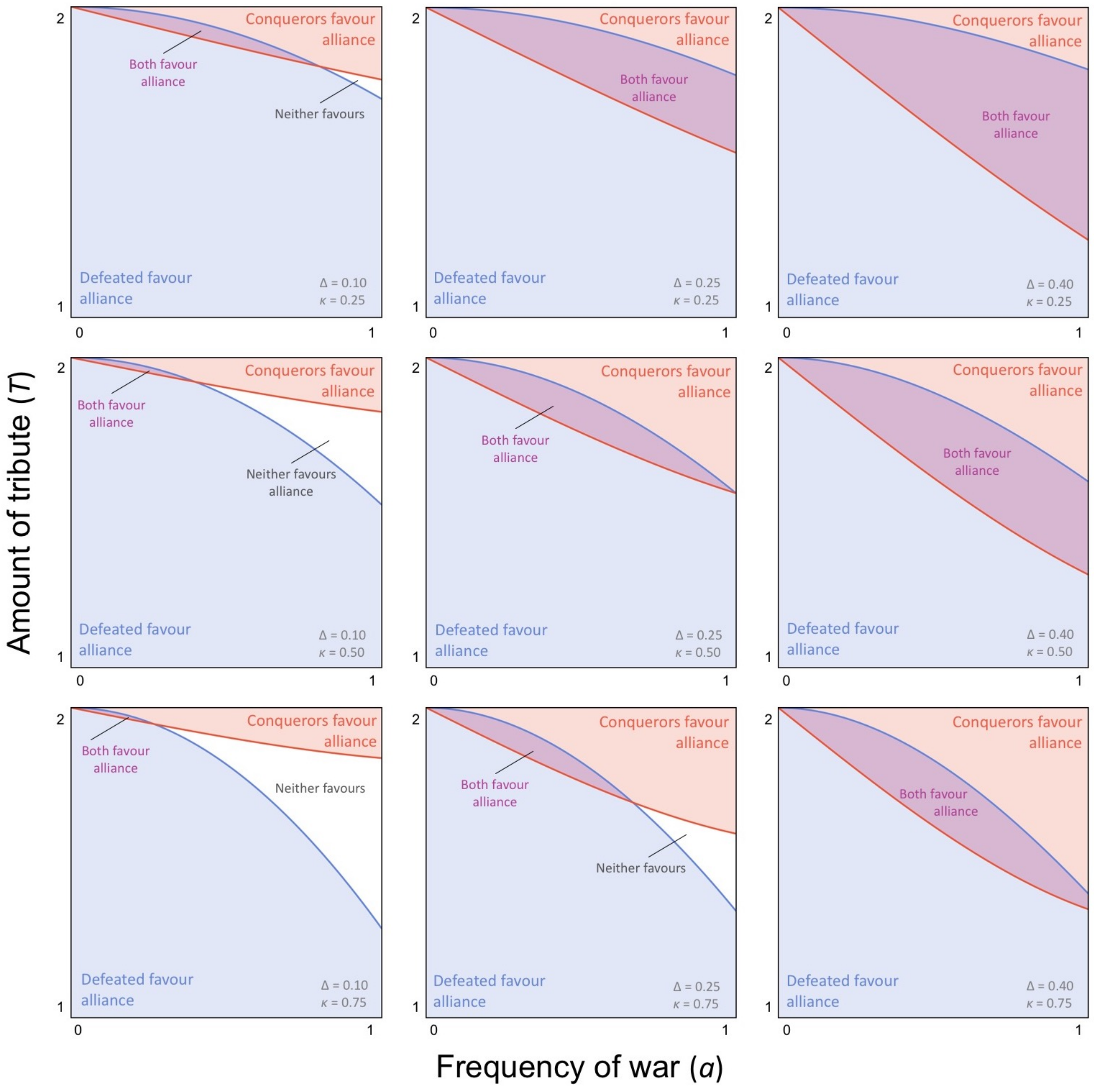

Figure 5.1 - Conflict over the tribute to be made by the defeated group to their conquerors. Minimum tolerated tribute threshold for the conquering group (red line) and maximum tolerated tribute threshold for the defeated group (blue line), as a function of war frequency a and for low, medium and high values of ally fatigue κ and increase in probability of success in war when fighting with an ally Δ. Alliance formation may be favoured by the conquering group alone (red shading), by the defeated group alone (blue shading), by both groups (purple shading) or by neither group (white) (see Extended Methods for details). Values obtained from conditions [5.1] and [5.2]; other parameter values: $m_\mathrm{m} = m_\mathrm{f} = 0.20$, $\omega_{11} = 0.50$, $\sigma_\mathrm{m} = 1$, $\bar{\lambda} = 0.50$.

associated with being pulled into additional wars. The net effect of this change in incentives is not a simple function of the incidence of war, and hence the scope for alliance need not be greater in more war-stricken populations (see Extended Methods for details). Instead, depending on the other factors in the ecology of war, intermediate frequencies of war might be the most conductive to alliance formation. All else being equal, a given level of tribute is more likely to be acceptable to both groups when having an ally results in greater chances of victory in future wars (large Δ) and when the negative effect of fatigue on the ally is limited (small κ) (see Fig. 5.1).

Our analysis so far has explored the conditions under which a conquering and a defeated group might find different levels of tribute acceptable or unacceptable. But what amount of tribute is actually ceded by the defeated side when accepting allegiance? To address this question, we model the formation of tribute demands from the conquering to the defeated group and explore how this process impacts on the likelihood of alliance formation. That is, having delineated the conflicting interests of the two groups, we now consider how these might be resolved (Godfray 1991, 1995].

We focus on the groups as the decision makers, following the approach adopted in previous work (Turchin and Gavrilets, 2009; Gavrilets, et al, 2010; Turchin, 2010]. We consider that the conquering group proposes an alliance to the defeated group, with the demand of a payment of tribute T, consisting of reproductive opportunities for men (for simplicity, but without loss of generality, we assume that women do not have access to reproductive opportunities in defeated groups; $\sigma_f = \tau_f = 0$). The conquerors collectively attempt to seize this amount of tribute – but, if this exceeds the maximum tolerated threshold for the vanquished side (T_{def}, obtained in the previous analysis), then the defeated group may not agree to form an alliance. The conquering group has the possibility to avoid this scenario by showing diplomacy, that is by seizing a lower amount of tribute (see Extended Methods for full details). We find that it is favoured for the victorious group to do so when:

$$-\bar{\lambda}\,c + \left(-S + T + B_{\mathrm{conq}}\,S\right)b > 0, \tag{5.3}$$

where $\bar{\lambda}$ is the population-wide average probability of alliance formation, *c* is the marginal loss of reproductive opportunities suffered by the conquering group as a consequence of it acting diplomatically, and *b* is the marginal increase in the probability of alliance formation due to decreased tribute demand. That is, by showing diplomacy, the conquering group lowers its tribute demand to the defeated group and thus: suffers a fitness cost *c* when an alliance is actually formed, which occurs with probability $\bar{\lambda}$ (first term in condition [5.3]); and increases the probability of forming an alliance by *b*, thus incurring the fitness effects associated with having an ally (second term) which were delineated in the previous analysis.

The optimal level of diplomacy for the conquering group may be obtained from condition [5.3], and from this the corresponding tribute demanded from the defeated group – which translates to an overall probability of alliance formation (see Extended Methods for details). We again find that a higher frequency of war (*a*) need not lead to alliances being more likely. Specifically, the conquering group may decrease their tribute demand most substantially at intermediate war intensities, whereas a very high frequency of war may result in unacceptable tribute requests that effectively prevent alliance formation (see Fig.

5.2). This result thus mirrors the one obtained in the previous analysis, and shows that greater overlap of interest between a conquering and a defending group results in them entering military alliances more often.

Having considered the interests of the group, we now consider the interests of individuals within the group and the conflicts that may arise between them. Consider that, in case of victory, each individual conqueror may attempt to seize reproductive opportunities for himself, for example in the form of resources or mates. Alternatively, they may show diplomacy and refrain from doing so – thus contributing to lowering the demands on the defeated group, and increasing the chances that this group forms an alliance with them. Analysing the model under this scenario – in which tribute demands are under 'individual control' – we find that young men in the conquering group are favoured to be diplomatic when:

$$-\bar{\lambda}\, c + \left(-S + T + B_{\mathrm{conq}}\, S\right) b\, r_{\mathrm{mm}} > 0, \qquad [5.4]$$

where r_{mm} is the genetic relatedness between male groupmates. That is, by being diplomatic, a young man in a conquering group pays a direct fitness cost $\bar{\lambda}\, c$ (first term in condition [5.4]) owing to having restrained from seizing reproductive opportunities for himself; but also incurs indirect fitness effects (second term) owing to a resulting increase in probability of alliance formation b, which may consequently translate to additional reproductive opportunities for young men in his group, who are related to him by r_{mm}.

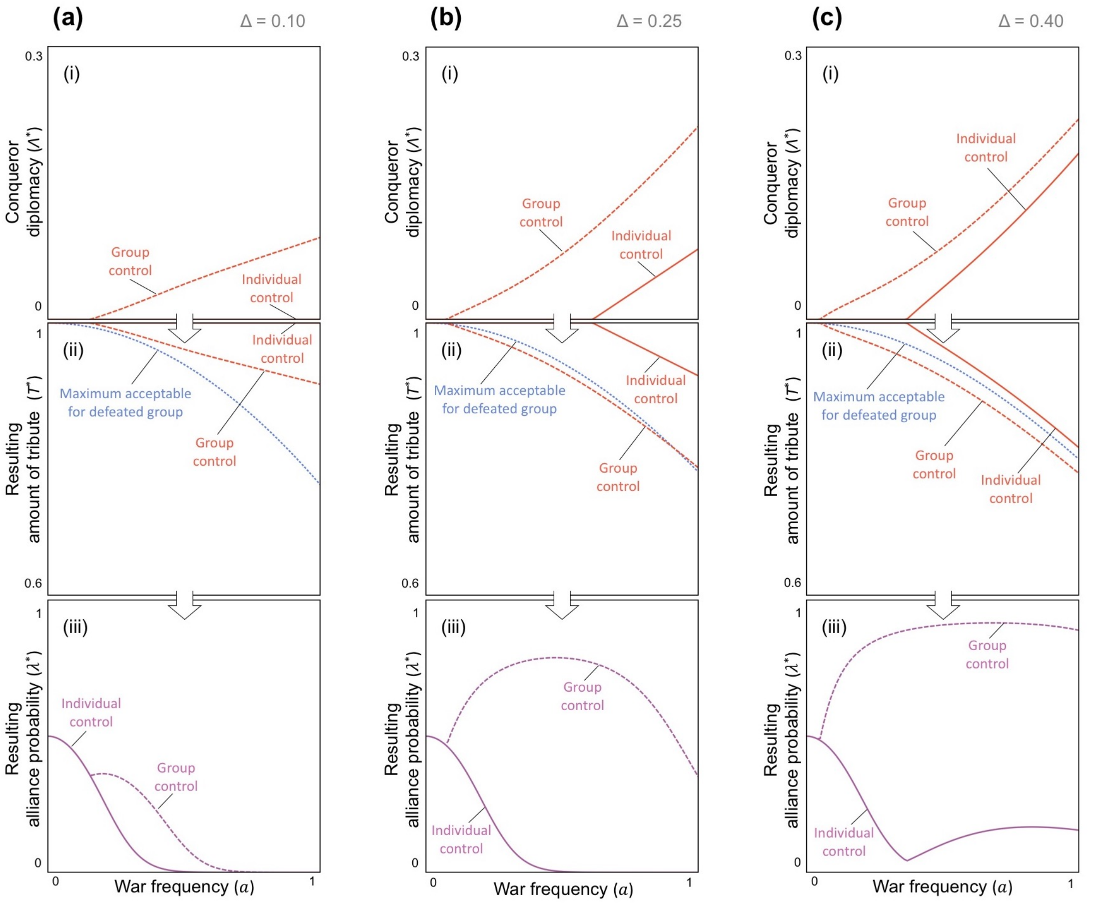

Figure 5.2 - Evolution of diplomacy and its consequences for the level of tribute and likelihood of alliance formation. Predicted levels of diplomacy for individual young men in a conquering group when acting in their own interest (solid red line; first row) or in their group's interest (dashed red line; first row); resulting amounts of tribute demanded by the conquering group under individual control (solid red line, second row) and group control (dashed red line), with the maximum tolerated tribute threshold for the defeated group (dotted blue line, second row); resulting probabilities of alliance formation when tribute demands from the conquering group are under individual control (solid purple line, third row) or group control (dashed purple line, third row) – as a function of war frequency *a* and for low, medium and high values of increase in probability of success in war when fighting with an ally Δ (panels a, b, and c, respectively). Values of diplomacy obtained from conditions [5.3] and [5.4], assuming functional forms $T = \sigma_m(1 - \Lambda_{conq})$ and $\lambda = 1/(1 + e^{-(T_{def} - T)/\epsilon})$ (see Extended Methods for details). other parameter values: $m_\mathrm{m} = m_\mathrm{f} = 0.20$, $\omega_{11} = 0.50$, $\Delta = 0.25$, $\kappa = 0.50$, $\sigma_\mathrm{m} = 1$, $\sigma_\mathrm{f} = \tau_\mathrm{f} = 0$, $N_\mathrm{m} = N_\mathrm{f} = 10$, $\epsilon = 0.01$.

In deciding whether to act diplomatically or not, the interests of the young man's group as a whole are set against his own individual interests, and while the costs associated with being diplomatic impact upon him directly, the group-level benefits of alliance formation affect his fitness only indirectly, and hence are devalued by his relatedness to groupmates.

Consideration of conditions [5.3] and [5.4] reveals scope for within-group conflict among conquerors over the tribute to be demanded of a defeated group. Specifically, the level of diplomacy predicted to evolve when individuals act in their own personal interest is always less than or equal to that which obtains when the decision is taken in the interest of the conquering group as a whole. This means that a conquering group demands a higher amount of tribute when the decision on level of tribute is an aggregate of selfish individual demands compared to when it reflects group-level interests – and thus, the probability of forming an alliance is lower when decisions are taken by single individuals than when they are taken at the level of the group (see Fig. 5.2). The demand of tribute thus represents a collective action problem that may substantially hinder the formation of between-group alliances.

Discussion

We have shown that a conquering and a defeated group may disagree over whether to form an alliance depending on the amount of tribute paid by the vanquished side, and that the tribute demanded by the conquering group tends to be higher – and thus the probability of alliance formation lower – when the conquerors act in their own individual interest, rather than in their group's. Taken together, the results of our analyses show that there is ample scope for conflicts of interest over the formation of military alliances between human groups and suggest that these conflicts may inhibit the major transition from smaller-scale human groups to larger multi-group societies. This transition has occurred in some parts of the globe since the end of the last Ice Age, while in others small foraging groups have remained dominant or the number of hierarchical (group-of-groups) levels has decreased (Currie, et al., 2010). Explaining the reasons behind these patterns and what drives the evolution of larger-scale multi-group societies are long-standing challenges in multiple disciplines (Diamond, 1997). While previous work has generally focused on the benefits afforded by the formation of larger multi-group polities through conquest and alliance formation (Turchin and Gavrilets, 2009; Gavrilets, et al., 2010; Turchin, 2010), here we have shown that conflicts of interest between and within different parties might be more important determinants of when major transitions in sociopolitical organisation occur and when they do not.

Previous studies of the emergence of larger multi-group societies via conquest, subordination or alliance formation have generally underlined the benefits gained by the victorious group in war in associating with a defeated group – with special stress on the advantages in future military confrontations afforded by the alliance (Turchin and Gavrilets, 2009; Gavrilets, et al., 2010; Turchin, 2010). We have shown that while these benefits can be substantial for the conquering group, they are reaped after the alliance is formed, they are conditional on the group actually being involved in a war, and are crucially modulated by the extent to which having an ally increases chances of success. Forming an alliance with a defeated group also entails an immediate and certain cost for the conquerors, as they agree to forgo unrestrained exploitation of the vanquished group's resources (thus allowing them to remain valuable as an ally) and accept a potentially less valuable tribute instead. We have shown that the benefits need not exceed the costs: in fact, this only occurs if the tribute is sufficiently large.

On the other hand, the perspective of the weaker party in the association – that is the group that has been defeated in battle – has previously been relatively neglected (Turchin and Gavrilets, 2009; Gavrilets, et al., 2010; Turchin, 2010). We have shown that, if a defeated group forms an alliance with their conqueror, they obtain an immediate and certain benefit – as they pay a tribute instead of suffering unrestrained exploitation – but also incur a potential cost in the future – as they risk being pulled into an additional war by their ally. In addition to the overall frequency of wars substantially influencing this balance, the extent of the tribute to be paid is once again crucial: if it is sufficiently small, an alliance may be worthwhile for the defeated group.

We have thus shown that conquering and defeated groups may be in conflict over whether to form an alliance, depending on the amount of tribute to be paid by the losers when the military association is formed. The existence of such between-group conflicts may significantly hinder the formation of alliances: as shown in the analysis of tribute demands from the conquerors, a smaller degree of overlap between the amounts of tribute acceptable to both groups translates to a lower probability that an alliance is formed. But did the interests of the defeated group matter in prehistorical small-scale societies or did conquerors simply coerce defeated groups into an alliance? Given that prehistorical human groups were characterised by simple political structure and no standing armed forces (Johnson and Earle, 2000; Gat, 2006), it seems virtually impossible that conquerors could enforce full cooperation of the vanquished group. Not demanding an exceedingly high tribute was most likely the only way to ensure that the ally did not defect, failing to provide military support – a possibility that was not considered in the present analysis and that constitutes an avenue for future exploration.

Our analysis has further revealed that whether or not amounts of tribute acceptable to both groups exist – and thus the formation of an alliance is possible – crucially depends on the ecology of war. We have focused especially on the rate of intergroup aggression, as this factor has received much attention in the literature and it has been suggested that elevated war frequencies – such as those found at the border between different ethnicities – led to the formation of larger multi-group polities and empires, through conquest, alliance or subordination (Turchin, 2010, 2015; Gavrilets, et al., 2010; Turchin and Gavrilets, 2009). Our results suggest that this might not always be the case. Indeed, we have shown that at high frequencies of war, there may be no amount of tribute that is acceptable to both parties, or the degree of overlap may be lower than when wars are less frequent. Further, modelling the formation of tribute demands from the conquering group, we have found that the probability of alliance formation may be highest when wars occur at intermediate frequencies, if some form of agreement is needed between the two parties.

We have found that other aspects of the ecology of war also influence alliance formation in significant ways, and that these interact with the frequency of war in determining outcomes. First, we have shown that, for a given frequency of war, groups are more likely to form a military association if having an ally substantially increases the group's chances of winning a war – as it is the case, for example, of war modes in which a group's fighting strength is proportional to the square of group size, while it increases only linearly with warrior effectiveness (a phenomenon termed 'Lanchester's square law'; Lanchester, 1916; Johnson and MacKay, 2015). In this sense, our analysis confirms previous verbal arguments that this war regime – realised for example when distance weapons, such as bow and arrow, are used – drives the formation of larger multi-group political entities through conquest, subordination, or alliance formation (Turchin, 2015). Second, we have shown that alliances are more likely to be formed when fighting an additional war has limited negative impact on the fitness of the defeated group that has been drawn into an alliance. This is not likely to be the case for prehistorical human societies, as warfare can result in a substantial number of casualties – over time, and relative to population sizes – in contemporary and historical hunter-gatherers (Keeley, 1997; Pinker, 2011; Glowacki, et al., 2017), and an even higher annual death rate in small-scale agricultural societies (Wrangham, et al, 2006). Therefore, considering that in our prehistorical past wars were likely costly in terms of individual fitness and were more likely to be won by larger armies, our analysis suggests that the highest probabilities of alliance formation would have been obtained for intermediate war frequencies (see Fig. 5.1 and 5.2).

Furthermore, we have shown that conflicts of interest over alliance formation are not limited to the between-group level, but may also arise within groups. Specifically, tribute negotiations represent a collective action problem for the conquering side: individual men benefit from demanding a larger tribute for themselves but, in so doing, increase the overall reproductive concessions requested to the defeated group, thus decreasing the chances that an alliance is formed – to the detriment of the whole group. In this way, conflicts between individual and group interests may inhibit the major transition to larger multi-group societies. This implies that such shifts to groups-of-groups – and by extension any polity with internal group structure, including tribes and chiefdoms (Service, 1962; Currie, et al., 2010) – could only have been achieved after within-group conflict in previously independent unites was resolved or suppressed. The results of our study suggest two – possibly mutually reinforcing – ways in which this might have happened in human groups that went on to became larger multi-group societies.

First, increased relatedness between groupmates could have led a narrowing gap between individual and group interests. In this way, men in the conquering group would have been favoured to act more diplomatically – i.e. altruistically – and restrain from seizing excessive reproductive opportunities from the defeated, helping to secure an alliance that benefitted other men they were closely related to. Low levels of dispersal, especially in men, together with small group sizes contribute to realising this outcome (see Extended Methods). Our analysis thus suggests that relatedness might have played a key role in determining the evolution of self-restraint in view of group interests – and parallels suggestions in the social insect literature. A large body of theoretical work and empirical evidence strongly suggests that the shift to eusocial societies was only possible after strict lifetime monogamy created a condition in which individuals are equally related to their own offspring and their sibling and so any slight advantage of helping behaviour is sufficient for its evolution (Crespi and Yanega 1995; Hughes, et al., 2008; Boomsma, et al., 2010; Boomsma, 2009; Fisher, et al., 2013; Davies and Gardner, 2018).

Second, complete or near-complete alignment of individual and group interests might have been achieved through suppression of within-group competition (Alexander, 1987; Frank, 2003). If individual men in the conquering group were barred from competing amongst themselves, they could only increase their reproductive success by enhancing the success of their group (Alexander, 1987; Frank, 2003). In this way, they could have been favoured to act diplomatically – to the benefit of the whole community. Mechanisms for suppression of competition include socially-imposed monogamy (leading to ‘reproductive opportunity levelling’) and laws guaranteeing equality of opportunity through policing (Alexander, 1987; Frank, 2003). These can lead to the evolution of altruism, and cooperation between individuals would have been possible in groups of increasing size and lower kinship (Alexander, 1987; Frank, 2003), or in small groups of weakly related individuals (like many contemporary hunter gatherers; Dyble, et al., 2015). In addition, Gavrilets and Fortunato (2014) have recently shown that within-group inequality in strength or leadership can resolve collective action problems in the context of warfare. A similar process might contribute to the prevailing of group interest in the negotiation of alliances.

Finally, we believe that our results are a contribution to the development of the theory of major evolutionary transitions in individuality. Our species is among the very few to engage in intergroup cooperation, a phenomenon that has received little attention so far, but that is witnessing a surge of interest (Robinson and Barker, 2017). In this study, we have provided formal analysis of such an interaction (Robinson and Barker, 2017), analysing conflicts of interest surrounding group-group cooperation in the context of its opposite: group-group competition. The existence of both kinds of interactions makes human societies invaluable to the study of when and how major transitions occur – or fail to do so – notwithstanding their complexities and challenges for investigation. In addition, instances in which human societies attempt to form higher-level groups when lower-level social structures have not yet achieved cohesion – e.g. largely failed attempts to form tribal confederations and states in Gaul and Germany during Roman times (Gat, 2006) –

constitute phenomena of great interest and add to examples of coexistence of conflict at multiple levels in other mammal societies (Clutton-Brock, 2016). Analysis of the selective pressure acting in these contexts can illuminate the fundamental processes behind major transitions and we hope that the analysis offered here will stimulate further work in this sense. For example, why is intergroup cooperation so rare? What is the role of conflicts between lower-level entities in explaining this? Beyond this, the study of human societal evolution as a major transition promises both to help us understand our history – from small bands to modern multi-ethnic states – and identify answers to global challenges – from climate change to growing inequality – that require cooperation and coordination at different levels.

Extended methods

Preamble

Here, we expand and adapt an existing kin-selection model of warfare (Lehmann and Feldman, 2008; Micheletti, et al., 2017, 2018; Chapter 2 and 3) to include the possibility of alliances arising between a conquering and a defeated group, with the latter ceding some reproductive success as tribute to the former and being compelled to aid them in a possible future war. We maintain the same fitness-generating events – i.e. instances of competition for reproductive opportunities – as the previous models, and allow for the formation of between-group alliances that modulate the probabilities that different fitness outcomes are obtained. We develop two models, adopting a 'battleground and resolution' approach which is widely used in behavioural ecological studies of animal behaviour (Godfray, 1991, 1995; Parker, 2006). In the first model (battleground), we identify the conditions under which a conquering and a defeated group may favour the formation of an alliance and assess potential for between-group conflict. In the second model (resolution), we assess possible outcomes of between-group conflict in terms of probability of alliance formation, by modelling negotiations between the two groups over the tribute value to be ceded by the defeated group – while also exploring potential for conflict within the conquering group over the amount to be demanded.

Summary

We adapt and expand an existing kin-selection model of warfare (Lehmann and Feldman, 2008; Micheletti, et al., 2017, 2018; Chapter 2 and 3) to study the selective pressures and potential conflicts of interest surrounding the formation of alliances between groups. We maintain the same fitness-generating events as the previous models (Lehmann and Feldman, 2008; Micheletti, et al., 2017, 2018; Chapters 2 and 3), and allow for the formation of between-group alliances that modulate the probabilities that different fitness outcomes are obtained. We develop two analyses to assess: a) the ecological conditions for potential conflicts of interest over alliance formation between a conquering and a defeated group ('group-group conflict model'); b) the outcomes of such conflicts in terms of probability of alliance formation mediated by tribute demands from the conquering group (Godfray, 1991, 1995), while also exploring potential within-group conflicts, namely between individual and group interests ('tribute demands model').

We consider an infinite population subdivided into groups of N_m adult men and N_f adult women. At the beginning of the life cycle, men and women mate randomly and each woman produces a large number K_m of sons and a large number K_f of daughters. These grow to become young adults, while the adults age to become non-reproductive elder men and women (we assume non-overlapping generations, following Lehmann and Feldman, 2008; Micheletti, et al., 2017, 2018; Chapters 2 and 3). Young adult men and women – hereafter, 'men' and 'women' – migrate to a randomly-chosen group with sex-specific probabilities, m_m and m_f. Groups may then engage in warfare: in each generation, we assume two rounds of attack. At the beginning of each generation, we select half of the groups at random to be 'attack-first' ('defend-second') groups and the other half to be 'defend-first' ('attack-second') groups. For conciseness, here we take the perspective of an attack-first group. First, every attack-first group has the opportunity to attack a defend-first group, with probability a. The attacking group wins the war with probability ω_{11} and an alliance with the defeated group may be formed with probability λ. Each attack-first group may then be itself attacked by a third randomly-chosen (defend-first) group, with probability a. The group successfully defends against attack with probability $1 - \omega_{11}$, if they did not form an alliance previously. This probability is increased by Δ if, instead, they have an ally (which is compelled to aid them in war). Density dependent competition follows the war phase. Members of attack-first groups that attacked another group and won against them compete for reproductive opportunities in that group against groupmates and defeated individuals of the same sex, with men having competitiveness σ_m and women σ_f (if an alliance between the two groups was not formed) or τ_m and τ_f (i.e. the tribute ceded by the defeated group if an alliance was formed). In addition, independently of the outcome of a possible attack war, members of attack-first groups that a) were not attacked or were attacked and successfully defended: compete for reproductive opportunities in their own group against groupmates of the same sex; b) were attacked and were defeated: compete for reproductive opportunities in their own group against groupmates and attackers of the same sex, with men having competitiveness $1 - \sigma_m$ and women $1 - \sigma_f$ (if their opponent was not pulled into an additional war by an ally) or $1 - (1 - \kappa)\sigma_m$ and $1 - (1 - \kappa)\sigma_f$ (if their opponent was pulled into an additional war). In addition, independently of the outcomes of defensive wars, members of attack-first groups that attacked another group and won against them compete for reproductive opportunities in that group against groupmates and defeated individuals of the same sex, with men having competitiveness σ_m and women σ_f (if an alliance between the two groups was not formed) or τ_m and τ_f (i.e. the tribute ceded by the defeated group if an alliance was formed).

In the group-group conflict model, we assess the ecological conditions under which a conquering and a defeated group may favour the formation of an alliance and potential conflicts of interest between the two parties. To do so, we hypothetically grant full control over alliance formation to the conquering group – determining the costs and benefits of alliance formation for them – and then we do the same for the defeated group (Godfray, 1991, 1995). We consider a trait $\mathcal{L}$ exhibited by individuals in either the conquering or the defeated group and we assume that the probability that an attacking group forms an alliance with a defeated group is given by $\lambda(\mathcal{L}_{\text{group}})$, where $\mathcal{L}_{\text{group}}$ is the trait level for individuals in the group under consideration. We perform a kin-selection analysis (Hamilton, 1964;

Taylor, 1996; Taylor and Frank 1996; Frank, 1997, 1998; Rousset, 2004; Taylor, et al., 2007) to determine how selection acts upon trait $\mathcal{L}$.

In the tribute demands model, we assess the potential outcome of conflicts of interest between an attacking and a defending group by modelling negotiations over the tribute to be paid by the defeated group. We consider that, if an alliance is formed, each man in a conquering group competes for breeding positions in a defeated group with competitiveness $\tau_{\text{ind}} = \sigma_{\text{m}}(1 - \Lambda_{\text{ind}})$, where Λ_{ind} is the diplomacy of the individual, and $-(\partial\tau_{\text{m,ind}}(\Lambda_{\text{ind}})/\partial\Lambda_{\text{ind}}) = c$ is the competitive cost of diplomacy for the individual man. Therefore, the overall tribute requested by the conquering group is given by $T = \tau_{\text{conq}} = \sigma_{\text{m}}(1 - \Lambda_{\text{conq}})$, where Λ_{conq} is the average diplomacy of members of the conquering group, and $(-(\partial\lambda(\tau_{\text{conq}})/\partial\tau_{\text{conq}})(-(\partial\tau_{\text{conq}}(\Lambda_{\text{conq}})/\partial\Lambda_{\text{conq}})) = b$ is the marginal increase in the probability of an alliance being formed with the defeated group. We perform a kin-selection analysis (Hamilton, 1964; Taylor, 1996; Taylor and Frank, 1996; Frank, 1997, 1998; Rousset, 2004; Taylor, et al., 2007) to determine how selection acts upon diplomacy Λ.

First model: group interests in alliance formation (battleground)

FITNESS

The relative fitness of a randomly-chosen individual of unspecified sex in a sex-structured population is given by $W = c_{\text{m}} W_{\text{m}} + c_{\text{f}} W_{\text{f}}$, which is an average of the fitness of male and female individuals weighted by their class reproductive values c_{m} and c_{f} (Fisher, 1930; Price and Smith, 1972; Taylor and Frank, 1996; Frank 1997; Taylor, et al., 2007). At the start of the life cycle, half of the groups are randomly selected as 'attack-first groups' and given the opportunity to attack another group from the other half ('defend-first groups'). The defend-first groups are then given the opportunity to attack another (attack-first) group (full details below). For this reason, each sex class is further divided into two sub-classes, 'members of attack-first groups' and 'members defend first groups'. The relative fitness of a randomly-chosen individual of unspecified sex can therefore be rewritten as:

$$W = c_{\text{m}}\left(\frac{\bar{w}_{\text{m,att}}}{\bar{w}_{\text{m,att}}+\bar{w}_{\text{m,def}}}W_{\text{m,att}} + \frac{\bar{w}_{\text{m,def}}}{\bar{w}_{\text{m,att}}+\bar{w}_{\text{m,def}}}W_{\text{m,def}}\right) + c_{\text{m}}\left(\frac{\bar{w}_{\text{m,att}}}{\bar{w}_{\text{m,att}}+\bar{w}_{\text{m,def}}}W_{\text{m,att}} + \frac{\bar{w}_{\text{m,def}}}{\bar{w}_{\text{m,att}}+\bar{w}_{\text{m,def}}}W_{\text{m,def}}\right) \quad \text{[A5.1]}$$

where the relative fitness for each sub-class is weighted by the ratio of the average fitness for that sub-class and the sum of average fitness for the two sub-classes in a given sex. Considered that $W_{\mathrm{i,j}} = w_{\mathrm{i,j}}/\bar{w}_{\mathrm{i,j}}$ (where i ∈{m,f} and j ∈{att,def}, and w is absolute fitness), equation [A5.1] can be rewritten as:

$$W = c_{\mathrm{m}}\widetilde{W}_{\mathrm{m,att}} + c_{\mathrm{m}}\widetilde{W}_{\mathrm{m,def}} + c_{\mathrm{f}}\widetilde{W}_{\mathrm{f,att}} + c_{\mathrm{f}}\widetilde{W}_{\mathrm{f,def}} \qquad \text{[A5.2]}$$

Where we term $\widetilde{W}_{\mathrm{i,j}} = w_{\mathrm{i,j}}/(\bar{w}_{\mathrm{m,j}} + \bar{w}_{\mathrm{f,j}})$ 'tilde-fitness' for a randomly-chosen individual of a given class.

Firstly, we derive the absolute fitness of a focal young adult of sex i ∈{m,f}, in the case that they are part of an attack-first group (see also life cycle described in Methods). With probability $1 - m_{\mathrm{i}}$, the focal young adult of sex-i does not migrate from the focal (attack-first) group. The war phase follows, and this is divided into two sub-phases. In the first sub-phase, the focal (attack-first) group can attack one randomly-chosen (defend-first) group. Three cases are possible, each leading to a potentially different second sub-phase:

> (i) With probability $1 - a$, the focal group does not attack the other group, and with probability $a(1 - \omega_{11})$ it attacks the other group but loses the war: in either case the focal sex-i young adult does not have access to breeding positions in the opponent group. The focal group then enters the second sub-phase of the life cycle, in which the group may be attacked by one other randomly-chosen group, different from the one they may have attacked in the first sub-phase. With probability $1 - a$ the focal group is not attacked by the other group, and with probability $a\ (1 - \omega_{11})$ it is attacked by the other group, but the attackers lose the war: in either case, the focal sex-i young adult competes for N_{i} breeding positions with $N_{\mathrm{f}}K_{\mathrm{i}}$ sex-i individuals (a fraction $1 - m_{\mathrm{i}}$ of which originated from the focal group and a fraction m_{i} migrated from another group and in this way the migration terms cancel out; N_{f} is the number of adult women in a group) such that their probability of securing a breeding spot is $N_{\mathrm{i}}/(N_{\mathrm{f}}K_{\mathrm{i}})$. Alternatively, with probability $a\omega_{11}$ the focal group is attacked by the

other group and the attackers win the war. In this case, with probability $1 - a^2\omega_{11}\bar{\lambda}$, the attacking group was not made an ally in the previous sub-phase or it was made an ally but was not pulled into an additional war, in which case the focal sex-i young adult competes for $(1 - \sigma_i) N_i$ breeding positions with $(1 - \sigma_i)N_f K_i$ sex-i young adults from their group and $\sigma_i N_f K_i$ from the attacking group, such that their probability of securing a breeding position is $(1 - \sigma_i)N_i/(N_f K_i)$. Alternatively, with probability $a^2\omega_{11}\bar{\lambda}$ the attacking group was made an ally in the previous sub-phase and was pulled into an additional war by their controlling ally, in which case the focal sex-i young adult competes for $(1 - (1 - \kappa)\sigma_i) N_i$ breeding positions with $(1 - (1 - \kappa)\sigma_i)N_f K_i$ sex-i young adults from their group and $(1 - \kappa)\sigma_i N_f K_i$ from the attacking group, such that their probability of securing a breeding position is $(1 - (1 - \kappa)\sigma_i)N_i/(N_f K_i)$.

(ii) With probability $a\omega 11(1 - \lambda)$, the focal group attacks another group, wins the war and an alliance between the two is not formed. In this case, the focal sex-i young adult competes for $\sigma_i N_i$ breeding spots with $\sigma_i N_f K_i$ sex-i young adults from their group and $(1 - \sigma_i)N_f K_i$ from the attacking group, such that their probability of securing a breeding spot is $\sigma_i N_i/(N_f K_i)$. The focal group then enters the second sub-phase of the life cycle, which – in this case – is identical to the one described in case (i) above.

(iii) With probability $a\omega_{11}\lambda$, the focal group attacks another group, wins the war and an alliance between the two is formed. In this case, the focal sex-i young adult competes for $\tau_i N_i$ breeding spots with $\tau_i N_f K_i$ sex-i young adults from their group and $(1 - \tau_i)N_f K_i$ from the attacking group, such that their probability of securing a breeding spot is $\tau_i N_i/(N_f K_i)$. The focal group then enters the second sub-phase of the life cycle, which – in this case – is identical to the one described in case (i) above, with the exception that the group which may attack the focal group wins the war with probability $\omega_{12} = \omega_{11} - \Delta$ (instead of ω_{11}) because the focal group has a subordinate ally (N.B. $\omega_{12} \leq \omega_{11}$).

Therefore, the absolute fitness of a focal sex-i young adult in an attack-first group is equal to:

$$\begin{aligned}
w_{\mathrm{i,att}} = {} & \left(1-a+a(1-\omega_{11})\right)\left(\left(1-a+a(1-\omega_{11})\right)+a\omega_{11}\left(\left(1-a^2\omega_{11}\bar{\lambda}\right)(1-\sigma_{\mathrm{i}})+a^2\omega_{11}\bar{\lambda}\left(1-(1-\kappa)\sigma_{\mathrm{i}}\right)\right)\right)\frac{N_{\mathrm{i}}}{N_{\mathrm{f}}K_{\mathrm{i}}} \\
& +a\omega_{11}(1-\lambda)\left(\sigma_{\mathrm{i}}+\left(1-a+a(1-\omega_{11})\right)+a\omega_{11}\left(\left(1-a^2\omega_{11}\bar{\lambda}\right)(1-\sigma_{\mathrm{i}})+a^2\omega_{11}\bar{\lambda}\left(1-(1-\kappa)\sigma_{\mathrm{i}}\right)\right)\right)\frac{N_{\mathrm{i}}}{N_{\mathrm{f}}K_{\mathrm{i}}} \\
& +a\omega_{11}\lambda\left(\tau_{\mathrm{i}}+\left(1-a+a(1-\omega_{12})\right)+a\omega_{12}\left(\left(1-a^2\omega_{11}\bar{\lambda}\right)(1-\sigma_{\mathrm{i}})+a^2\omega_{11}\bar{\lambda}\left(1-(1-\kappa)\sigma_{\mathrm{i}}\right)\right)\right)\frac{N_{\mathrm{i}}}{N_{\mathrm{f}}K_{\mathrm{i}}} \qquad \text{[A5.3]}
\end{aligned}$$

Secondly, we derive the absolute fitness of a focal young adult of sex i $\in\{m,f\}$, in the case that they are part of a defend-first group. With probability $1 - m_i$, the focal young adult of sex-i does not migrate from the focal (defend-first) group. The war phase follows. In the first sub-phase, the focal (defend-first) group may be attacked by one randomly-chosen (attack-first) group. Three cases are possible, each leading to a potentially different second sub-phase:

> (i) With probability $1 - a$, the focal group is not attacked by the other group, and with probability $a(1 - \omega_{11})$ it is attacked by the other group but the attackers lose the war: in either case the focal sex-i young adult competes for N_i breeding positions in his group with $N_f K_i$ sex-i young adults such that their probability of securing a breeding spot is $N_i/(N_f K_i)$. The focal group then enters the second sub-phase of the life cycle, in which the group can attack one other randomly-chosen group, different from the one that may have attacked them in the first sub-phase. With probability $1 - a$, the focal group does not attack the other group, in which case the focal sex-i young adult does not have access to additional breeding positions in the opponent group. Alternatively, with probability a, the focal group attacks the other group. In this case, with probability $1 - a^2\omega_{11}\bar{\lambda}$, the attacked group does not have an ally: the focal group loses the war with probability $1 - \omega_{11}$ (and the focal sex-i individual does not have access to breeding positions in the opponent group) or wins the war with probability ω_{11} (and the focal sex-i individual secures a breeding position in the opponent group with probability $\sigma_i N_i/(N_f K_i)$). Alternatively, with probability $a^2\omega_{11}\bar{\lambda}$, the attacked group does has an ally: the focal group loses the war with

probability $1 - \omega_{12}$ (and the focal sex-i individual does not have access to breeding positions in the opponent group) or wins the war with probability ω_{12} (and the focal sex-i individual secures a breeding position in the opponent group with probability $\sigma_i N_i/(N_f K_i)$).

(ii) With probability $a\omega 11(1 - \lambda)$, the focal group is attacked by another group, the attacker wins the war and an alliance between the two is not formed. In this case, the focal sex-i young adult competes for $(1 - \sigma_i)N_i$ breeding spots in their group with $(1 - \sigma_i)N_f K_i$ sex-i young adults from their group and $\sigma_i N_f K_i$ from the attacking group, such that their probability of securing a breeding spot is $(1 - \sigma_i)N_i/(N_f K_i)$. The focal group then enters the second sub-phase of the life cycle, which – in this case – is identical to the one described in case (i) above.

(iii) With probability $a\omega_{11}\lambda$, the focal group is attacked by another group, the attacker wins the war and an alliance between the two is formed. In this case, the focal sex-i young adult competes for $(1 - \tau_i)N_i$ breeding spots in their group with $(1 - \tau_i)N_f K_i$ sex-i young adults from their group and $\tau_i N_f K_i$ from the attacking group, such that their probability of securing a breeding spot is $(1 - \tau_i)N_i/(N_f K_i)$. The focal group then enters the second sub-phase of the life cycle. With probability $1 - a$, the focal group is not pulled into an additional war by the ally (i.e. their ally is not attacked). In this case, the second sub-phase is identical to the one described in case (i) immediately above. Alternatively, with probability a, the focal group is pulled into an additional wat by their ally (i.e. their ally is attacked). In this case, the second sub-phase is identical to the one described in case (i) above, with the exception that the focal sex-i individual secures a breeding position in a defeated group with probability $(1 - \kappa)\sigma_i N_i/(N_f K_i)$ (instead of $\sigma_i N_i/(N_f K_i)$) because of the effect of fatigue associated with having fought an additional war.

Therefore, the absolute fitness of a focal young adult male in a defend-first group is equal to:

$$\begin{aligned}w_{\mathrm{i,def}} &= \left(1 - a + a(1 - \omega_{11})\right)\left(1 + a\left(\left(1 - a^2\omega_{11}\bar{\lambda}\right)\omega_{11}\sigma_{\mathrm{i}} + a^2\omega_{11}\bar{\lambda}\omega_{12}\sigma_{\mathrm{i}}\right)\right)\frac{N_{\mathrm{i}}}{N_{\mathrm{f}}K_{\mathrm{i}}}\\ &+ a\omega_{11}(1 - \lambda)\left((1 - \sigma_{\mathrm{i}}) + a\left(\left(1 - a^2\omega_{11}\bar{\lambda}\right)\omega_{11}\sigma_{\mathrm{i}} + a^2\omega_{11}\bar{\lambda}\omega_{12}\sigma_{\mathrm{i}}\right)\right)\frac{N_{\mathrm{i}}}{N_{\mathrm{f}}K_{\mathrm{i}}}\\ &+ a\omega_{11}\lambda\left((1 - \tau_{\mathrm{i}}) + (1 - a)\left(a\left(\left(1 - a^2\omega_{11}\bar{\lambda}\right)\omega_{11}\sigma_{\mathrm{i}} + a^2\omega_{11}\bar{\lambda}\omega_{12}\sigma_{\mathrm{i}}\right)\right) + a\left(a\left(\left(1 - a^2\omega_{11}\bar{\lambda}\right)\omega_{11}(1 - \kappa)\sigma_{\mathrm{i}} + a^2\omega_{11}\bar{\lambda}\omega_{12}(1 - \kappa)\sigma_{\mathrm{i}}\right)\right)\right)\frac{N_{\mathrm{i}}}{N_{\mathrm{f}}K_{\mathrm{i}}}\end{aligned} \quad [A5.4]$$

The sum of the average fitness for the attack-first and the defend first class for a given sex is $\bar{w}_{\mathrm{i,att}} + \bar{w}_{\mathrm{i,def}} = 2N_{\mathrm{i}}/(N_{\mathrm{f}}K_{\mathrm{i}})$. The tilde-fitness of a focal sex-i young adult who is part of a j-first group is given by $\widetilde{W}_{\mathrm{i,j}} = w_{\mathrm{i,j}}/(2N_{\mathrm{i}}/(N_{\mathrm{f}}K_{\mathrm{i}}))$, where i ∈{m,f} and j ∈{att,def}.

ALLIANCE FORMATION – MARGINAL FITNESS

Consider a locus $\mathcal{G}$, which controls a trait $\mathcal{L}$ which may be expressed by young adults of either sex. We denote the genic value of the focal individual for this gene by *g*, the breeding value of the ‘controller’ (i.e. the individual controlling the phenotype) by *G*, the breeding value of a groupmate’s controller by *G*', and the population average breeding value by $\bar{G}$. Assuming vanishing genetic variation – all breeding values of the population are tightly clustered around the mean (Taylor and Frank, 1996; Frank, 1997), the direction of natural selection is given by:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_{\mathrm{m}}\frac{\mathrm{d}\widetilde{W}_{\mathrm{m,att}}}{\mathrm{d}g_{\mathrm{m,att}}} + c_{\mathrm{m}}\frac{\mathrm{d}\widetilde{W}_{\mathrm{m,def}}}{\mathrm{d}g_{\mathrm{m,def}}} + c_{\mathrm{f}}\frac{\mathrm{d}\widetilde{W}_{\mathrm{f,att}}}{\mathrm{d}g_{\mathrm{f,att}}} + c_{\mathrm{f}}\frac{\mathrm{d}\widetilde{W}_{\mathrm{f,def}}}{\mathrm{d}g_{\mathrm{f,def}}} \quad [A5.5]$$

The derivative $\mathrm{d}\widetilde{W}_{\mathrm{i,j}}/\mathrm{d}g_{\mathrm{i,j}}$ describes the impact of the genic value of a gene drawn from a sex-i young adult in a j-first group on their tilde-fitness, where where i ∈{m,f} and j ∈{att,def}. Employing the chain rule, we expand it, obtaining:

$$\frac{\mathrm{d}\widetilde{W}_{\mathrm{i,j}}}{\mathrm{d}g_{\mathrm{i,j}}} = \frac{\partial\widetilde{W}_{\mathrm{i,j}}}{\partial\mathcal{L}}\frac{\mathrm{d}\mathcal{L}}{\mathrm{d}G}\frac{\mathrm{d}G}{\mathrm{d}g_{\mathrm{i,j}}} + \frac{\partial\widetilde{W}_{\mathrm{i,j}}}{\partial\mathcal{L}'}\frac{\mathrm{d}\mathcal{L}'}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_{\mathrm{i,j}}} = \left(\frac{\partial\widetilde{W}_{\mathrm{i,j}}}{\partial\mathcal{L}}p_{\mathrm{i,j}|\mathcal{A}} + \frac{\partial\widetilde{W}_{\mathrm{i,j}}}{\partial\mathcal{L}'}p_{\mathrm{i,j|A}}\right)\gamma \quad [A5.6]$$

where $\partial\widetilde{W}_{\mathrm{i,j}}/\mathrm{d}\mathcal{L}$ is the impact of the phenotype of the focal sex-i individual in a j-first group on their tilde-fitness, $\partial\widetilde{W}_{\mathrm{i,j}}/\mathrm{d}\mathcal{L}'$ is the impact of the phenotype of a random sex-i individual in the focal j-first group on the fitness of the focal sex-i individual in the same j-first group, $p_{\mathrm{i,j}|\mathcal{A}} = \mathrm{d}G/\mathrm{d}g_{\mathrm{i,j}}$ is the consanguinity of the controller of the focal sex-i individual in the focal j-first group of sex i (denoted by $\mathcal{A}$) to that focal individual, $p_{\mathrm{i,j|A}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{i,j}}$ is the consanguinity between the controller of a random sex-i individual in the focal j-first group (denoted by A) to focal individual, and $\gamma = \mathrm{d}\mathcal{L}/\mathrm{d}G = \mathrm{d}\mathcal{L}'/\mathrm{d}G'$ is the correlation between an individual's phenotype and the breeding value of their controller.

We assume that the phenotype $\mathcal{L}$ does not impact on the tilde-fitness of the individual – that is there is no direct fitness impact – therefore $\partial\widetilde{W}_{\mathrm{i,j}}/\mathrm{d}\mathcal{L} = 0$. We consider that the probability that the focal group forms an alliance in the first sub-phase of the life cycle λ is a function of $\mathcal{L}$ (see Methods). Therefore $\partial\widetilde{W}_{\mathrm{i,j}}/\mathrm{d}\mathcal{L}' = (\partial\widetilde{W}_{\mathrm{i,j}}/\mathrm{d}\lambda)(\mathrm{d}\lambda/\mathrm{d}\mathcal{L}')$. Substituting this and [A5.6] into [A5.5], we obtain:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_{\mathrm{m}}\frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\lambda}\frac{\partial\lambda}{\partial\mathcal{L}'}p_{\mathrm{m,att|A}}\gamma + c_{\mathrm{m}}\frac{\partial\widetilde{W}_{\mathrm{m,def}}}{\partial\lambda}\frac{\partial\lambda}{\partial\mathcal{L}'}p_{\mathrm{m,def|A}}\gamma + c_{\mathrm{f}}\frac{\partial\widetilde{W}_{\mathrm{f,att}}}{\partial\lambda}\frac{\partial\lambda}{\partial\mathcal{L}'}p_{\mathrm{f,att|A}}\gamma + c_{\mathrm{f}}\frac{\partial\widetilde{W}_{\mathrm{f,def}}}{\partial\lambda}\frac{\partial\lambda}{\partial\mathcal{L}'}p_{\mathrm{f,def|A}}\gamma \quad \text{[A5.7]}$$

The condition for an increase in population average $\mathcal{L}$ is $\mathrm{d}W/\mathrm{d}g > 0$ (in Results for simplicity and greater clarity we term this the condition under which a 'group favours the formation of an alliance'). Considering that $c_{\mathrm{f}} = c_{\mathrm{m}} = 1/2$ under diploid inheritance, this condition is given by:

$$\frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\lambda}p_{\mathrm{m,att|A}} + \frac{\partial\widetilde{W}_{\mathrm{m,def}}}{\partial\lambda}p_{\mathrm{m,def|A}} + \frac{\partial\widetilde{W}_{\mathrm{f,att}}}{\partial\lambda}p_{\mathrm{f,att|A}} + \frac{\partial\widetilde{W}_{\mathrm{f,def}}}{\partial\lambda}p_{\mathrm{f,def|A}} > 0 \quad \text{[A5.8]}$$

If the controller is a class of individuals or a randomly-chosen individual in any class within the attack-first group (young adult men/women, elder men/women, see CONFLICTS

OF INTEREST), the consanguinities between the controller and male or female individuals in the defend-first group are null. Therefore condition [A5.8] above simplifies to:

$$\frac{\partial \widetilde{W}_{\mathrm{m,att}}}{\partial \lambda} p_{\mathrm{m,att|A}} + \frac{\partial \widetilde{W}_{\mathrm{f,att}}}{\partial \lambda} p_{\mathrm{f,att|A}} > 0 \qquad \text{[A5.9]}$$

Dividing by p_{self} to obtain $p_{\mathrm{m,att|A}}/p_{\mathrm{self}} = p_{\mathrm{m|A}}/p_{\mathrm{self}} = \mathrm{r}_{\mathrm{m|A}}$ and $p_{\mathrm{f,att|A}}/p_{\mathrm{self}} = p_{\mathrm{f|A}}/p_{\mathrm{self}} = \mathrm{r}_{\mathrm{f|A}}$ (see CONSANGUINITY AND RELATEDNESS) and making derivatives explicit yields:

$$\begin{aligned}&\left(-(\sigma_{\mathrm{m}} - \tau_{\mathrm{m}}) + a\Delta\left(1 - a^2\omega_{11}\bar{\lambda} + (1-\kappa)a^2\omega_{11}\bar{\lambda}\right)\sigma_{\mathrm{m}}\right) r_{\mathrm{m|A}} \\ &+ (-(\sigma_{\mathrm{f}} - \tau_{\mathrm{f}}) + a\Delta\left(1 - a^2\omega_{11}\bar{\lambda} + (1-\kappa)a^2\omega_{11}\bar{\lambda}\right)\sigma_{\mathrm{f}}) r_{\mathrm{f|A}} > 0 \qquad \text{[A5.10]}\end{aligned}$$

Rearranging terms:

$$-\left((\sigma_{\mathrm{m}} - \tau_{\mathrm{m}}) r_{\mathrm{m|A}} + (\sigma_{\mathrm{f}} - \tau_{\mathrm{f}}) r_{\mathrm{f|A}}\right) + a\Delta\left(1 - a^2\omega_{11}\bar{\lambda} + (1-\kappa)a^2\omega_{11}\bar{\lambda}\right)(\sigma_{\mathrm{m}} r_{\mathrm{m|A}} + \sigma_{\mathrm{f}} r_{\mathrm{f|A}}) > 0 \qquad \text{[A5.11]}$$

That is, if an alliance is formed, members of the class of individuals in the conquering group under consideration incur: an indirect fitness cost (first term) accrued in the first sub-phase due to a $\sigma_{\mathrm{m}} - \tau_{\mathrm{m}}$ loss of reproductive success for young adult men who are related by $r_{\mathrm{m|A}}$ to members of the focal class of individuals and a $\sigma_{\mathrm{f}} - \tau_{\mathrm{f}}$ loss of reproductive success for young adult women who are related by $r_{\mathrm{f|A}}$; an indirect fitness benefit (second term) accrued in the second sub-phase – specifically when the group is attacked, with probability a – due to an increased chance $\Delta = \omega_{11} - \omega_{12}$ of winning against the defensive war and thus preserving σ_{m} reproductive success for young adult men and σ_{f} reproductive success for young adult females (in the case in which the attacking group was not pulled into an additional war by their ally, which occurs with probability $1 - a^2\omega_{11}\bar{\lambda}$) or preserving $(1 - \kappa)\sigma_{\mathrm{m}}$ and $(1 - \kappa)\sigma_{\mathrm{f}}$ reproductive success (in the case in which the attacking group was pulled into an additional war by their ally, which occurs with probability$a^2\omega_{11}\bar{\lambda}$).

Dividing condition [A5.11] by $\mathrm{r}_{\mathrm{m|A}}$ – thus obtaining $v = \mathrm{r}_{\mathrm{f|A}}/\mathrm{r}_{\mathrm{m|A}}$ – and rearranging terms, yields condition [5.1] in Results, where $B_{\mathrm{conq}} = a\Delta(1 - a^2\omega_{11}\bar{\lambda} + (1-\kappa)a^2\omega_{11}\bar{\lambda})$.

Analogously, if the controller is a class of individuals or a randomly-chosen individual in any class within the defend-fist group (young adult men/women, elder men/women, see CONFLICTS OF INTEREST), the consanguinities between the controller and male or female individuals in the attack-first group are null. Therefore condition [A5.8] reduces to:

$$\frac{\partial \widetilde{W}_{\mathrm{m,def}}}{\partial \lambda} p_{\mathrm{m,def|A}} + \frac{\partial \widetilde{W}_{\mathrm{f,def}}}{\partial \lambda} p_{\mathrm{f,def|A}} > 0 \qquad [A5.12]$$

Dividing by p_{self} to obtain $p_{\mathrm{m,def|A}}/p_{\mathrm{self}} = p_{\mathrm{m|A}}/p_{\mathrm{self}} = \mathrm{r}_{\mathrm{m|A}}$ and $p_{\mathrm{f,def|A}}/p_{\mathrm{self}} = p_{\mathrm{f|A}}/p_{\mathrm{self}} = \mathrm{r}_{\mathrm{f|A}}$ (see CONSANGUINITY AND RELATEDNESS) and making derivatives explicit yields:

$$\begin{aligned}&\Big((\sigma_{\mathrm{m}} - \tau_{\mathrm{m}}) - a^2\kappa\Big(\big(1 - a\omega_{11}\bar{\lambda}\big)\omega_{11} + a\omega_{11}\bar{\lambda}\omega_{12}\Big)\sigma_{\mathrm{m}}\Big)p_{\mathrm{m,def|A}}\\ &+\Big((\sigma_{\mathrm{f}} - \tau_{\mathrm{f}}) - a^2\kappa\Big(\big(1 - a\omega_{11}\bar{\lambda}\big)\omega_{11} + a\omega_{11}\bar{\lambda}\omega_{12}\Big)\sigma_{\mathrm{f}}\Big)p_{\mathrm{f,def|A}} > 0 \qquad [A5.13]\end{aligned}$$

Rearranging terms:

$$(\sigma_{\mathrm{m}} - \tau_{\mathrm{m}})r_{\mathrm{m|A}} + (\sigma_{\mathrm{f}} - \tau_{\mathrm{f}})r_{\mathrm{f|A}} - a^2\kappa\Big(\big(1 - a\omega_{11}\bar{\lambda}\big)\omega_{11} + a\omega_{11}\bar{\lambda}\omega_{12}\Big)(\sigma_{\mathrm{m}}r_{\mathrm{m|A}} + \sigma_{\mathrm{f}}\, r_{\mathrm{f|A}}) > 0 \qquad [A5.14]$$

That is, if an alliance is formed, members of the class of individuals in a defend-first group under consideration incur: an indirect fitness benefit (first term) accrued in the first sub-phase due to a $\sigma_{\mathrm{m}} - \tau_{\mathrm{m}}$ gain (decreased loss) of reproductive success for young adult males who are related by $r_{\mathrm{m|A}}$ to members of the focal class of individuals and a $\sigma_{\mathrm{f}} - \tau_{\mathrm{f}}$ gain (decreased loss) of reproductive success for young adult females group-mates who are related by $r_{\mathrm{m|A}}$; an indirect fitness cost (second term) accrued in the second sub-phase – specifically when the focal group attacks another group with probability *a*, and their ally is attacked by another group, also with probability *a*, and thus the focal group is pulled into an additional war – due to a decreased gain in reproductive success $\sigma_{\mathrm{m}} - (1-\kappa)\sigma_{\mathrm{m}} = \kappa\sigma_{\mathrm{m}}$ for young adult males and $\kappa\sigma_{\mathrm{f}}$ for young adult females, which is obtained with probability ω_{11} (in case the attacked group does not have a subordinate ally, which occurs with probability $1 - a\omega_{11}\bar{\lambda}$) or with probability ω_{12} (in case the attacked group has a subordinate ally, which occurs with probability $a\omega_{11}\bar{\lambda}$).

Dividing condition [A5.14] by $r_{\mathrm{m|A}}$ and rearranging terms, yields condition [5.2] in Results, where $C_{\mathrm{def}} = a^2\kappa\big((1 - a\omega_{11}\bar{\lambda})\omega_{11} + a\omega_{11}\bar{\lambda}\omega_{12}\big)$.

CONSANGUINITY AND RELATEDNESS

The coefficient of consanguinity between two individuals A and B at a given locus, p_{AB}, is equal to the probability of identity-by-descent between a gene randomly-drawn from that locus in individual A and a gene randomly-drawn from the same locus in individual B (Bulmer, 1994). In the case in which the second individual coincides with the first, i.e. B=A, the consanguinity of an individual to themselves is obtained and it is given by $p_{\mathrm{self}} = (1+f)/2$. The consanguinity between two adult mating partners, one from each sex, in a post-competition group (independently of whether this was an attack-first or defend-first group) is termed inbreeding coefficient and is given by $f = \varphi_{\mathrm{mf}}\, p_{\mathrm{x}}$. Analogously, the consanguinity of two sex-i adults in a post-competition group is given by $p_{\mathrm{ii,adult}} = \varphi_{\mathrm{ii}}\, p_{\mathrm{x}}$, where $\mathrm{i} \in \{\mathrm{m,f}\}$. The coefficients φ_{mf} and φ_{ii} are the probabilities that two adults of opposite sex and two sex-i adults, respectively, who are in the same post-competition group, were born in the same group and are given by:

$$\begin{aligned}
&\varphi_{\mathrm{mf}} = \tfrac{1}{2}\Big((1-a+a(1-\omega_{11}))\Big((1-a+a(1-\omega_{11})) + a\omega_{11}((1-a^2\omega_{11}\lambda)(1-\sigma_{\mathrm{m}})(1-\sigma_{\mathrm{f}}) + a^2\omega_{11}\lambda(1-(1-\kappa)\sigma_{\mathrm{m}})(1-(1-\kappa)\sigma_{\mathrm{f}}))\Big) + a\omega_{11}(1- \\
&\lambda)\Big(\sigma_{\mathrm{m}}\sigma_{\mathrm{f}} + (1-a+a(1-\omega_{11})) + a\omega_{11}((1-a^2\omega_{11}\lambda)(1-\sigma_{\mathrm{m}})(1-\sigma_{\mathrm{f}}) + a^2\omega_{11}\lambda(1-(1-\kappa)\sigma_{\mathrm{m}})(1-(1-\kappa)\sigma_{\mathrm{f}}))\Big) + +a\omega_{11}\lambda\Big(\tau_{\mathrm{m}}\tau_{\mathrm{f}} + (1-a+a(1-\omega_{12})) + \\
&a\omega_{12}((1-a^2\omega_{11}\lambda)(1-\sigma_{\mathrm{m}})(1-\sigma_{\mathrm{f}}) + a^2\omega_{11}\lambda(1-(1-\kappa)\sigma_{\mathrm{m}})(1-(1-\kappa)\sigma_{\mathrm{f}}))\Big)\Big) + \tfrac{1}{2}\Big((1-a+a(1-\omega_{11}))\Big(1 + a((1-a^2\omega_{11}\lambda)\omega_{11}\sigma_{\mathrm{m}}\sigma_{\mathrm{f}} + \\
&a^2\omega_{11}\lambda\omega_{12}\sigma_{\mathrm{m}}\sigma_{\mathrm{f}})\Big) + a\omega_{11}(1-\lambda)\Big((1-\sigma_{\mathrm{m}})(1-\sigma_{\mathrm{f}}) + a((1-a^2\omega_{11}\lambda)\omega_{11}\sigma_{\mathrm{m}}\sigma_{\mathrm{f}} + a^2\omega_{11}\lambda\omega_{12}\sigma_{\mathrm{m}}\sigma_{\mathrm{f}})\Big) + a\omega_{11}\lambda\Big((1-\tau_{\mathrm{m}})(1-\tau_{\mathrm{f}}) + (1-a)\Big(a((1- \\
&a^2\omega_{11}\lambda)\omega_{11}\sigma_{\mathrm{m}}\sigma_{\mathrm{f}} + a^2\omega_{11}\lambda\omega_{12}\sigma_{\mathrm{m}}\sigma_{\mathrm{f}})\Big) + a\Big(a((1-a^2\omega_{11}\lambda)\omega_{11}(1-\kappa)^2\sigma_{\mathrm{m}}\sigma_{\mathrm{f}} + a^2\omega_{11}\lambda\omega_{12}(1-\kappa)^2\sigma_{\mathrm{m}}\sigma_{\mathrm{f}})\Big)\Big)\Big), \qquad [\mathrm{A}5.15]
\end{aligned}$$

and:

$$\begin{gathered}\varphi_{\mathrm{ii}} = \frac{1}{2}\Big(\big(1-a+a(1-\omega_{11})\big)\Big(\big(1-a+a(1-\omega_{11})\big)+a\omega_{11}\big((1-a^2\omega_{11}\lambda)(1-\sigma_{\mathrm{i}})^2+a^2\omega_{11}\lambda(1-(1-\kappa)\sigma_{\mathrm{i}})^2\big)\Big)+a\omega_{11}(1-\lambda)\Big({\sigma_{\mathrm{i}}}^2+\big(1-a+a(1-\omega_{11})\big)+ \\ a\omega_{11}\big((1-a^2\omega_{11}\lambda)(1-\sigma_{\mathrm{i}})^2+a^2\omega_{11}\lambda(1-(1-\kappa)\sigma_{\mathrm{i}})^2\big)\Big)++a\omega_{11}\lambda\Big({\tau_{\mathrm{i}}}^2+\big(1-a+a(1-\omega_{12})\big)+a\omega_{12}\big((1-a^2\omega_{11}\lambda)(1-\sigma_{\mathrm{i}})^2+a^2\omega_{11}\lambda(1-(1-\kappa)\sigma_{\mathrm{i}})^2\big)\Big)\Big)+ \\ \frac{1}{2}\Bigg(\big(1-a+a(1-\omega_{11})\big)\Big(1+a\big((1-a^2\omega_{11}\lambda)\omega_{11}{\sigma_{\mathrm{i}}}^2+a^2\omega_{11}\lambda\omega_{12}{\sigma_{\mathrm{i}}}^2\big)\Big)+a\omega_{11}(1-\lambda)\Big((1-\sigma_{\mathrm{i}})^2+a\big((1-a^2\omega_{11}\lambda)\omega_{11}{\sigma_{\mathrm{i}}}^2+a^2\omega_{11}\lambda\omega_{12}{\sigma_{\mathrm{i}}}^2\big)\Big)+a\omega_{11}\lambda\Bigg((1- \\ \tau_{\mathrm{i}})^2+(1-a)\Big(a\big((1-a^2\omega_{11}\lambda)\omega_{11}{\sigma_{\mathrm{i}}}^2+a^2\omega_{11}\lambda\omega_{12}{\sigma_{\mathrm{i}}}^2\big)\Big)+a\Big(a\Big((1-a^2\omega_{11}\lambda)\omega_{11}\big((1-\kappa)\sigma_{\mathrm{i}}\big)^2+a^2\omega_{11}\lambda\omega_{12}\big((1-\kappa)\sigma_{\mathrm{i}}\big)^2\Big)\Big)\Bigg)\Bigg), \qquad [\mathrm{A}5.16]\end{gathered}$$

respectively. p_{X} is the consanguinity of individuals born in the same group and is given by:

$$p_{\mathrm{X}} = \frac{1}{4}\left(\frac{1}{N_{\mathrm{m}}}p_{\mathrm{self}} + \frac{N_{\mathrm{m}}-1}{N_{\mathrm{m}}}p_{\mathrm{mm,adult}}\right) + \frac{1}{2}f + \frac{1}{4}\left(\frac{1}{N_{\mathrm{f}}}p_{\mathrm{self}} + \frac{N_{\mathrm{f}}-1}{N_{\mathrm{f}}}p_{\mathrm{ff,adult}}\right) \qquad [\mathrm{A}5.17]$$

which, substituting the appropriate consanguinities and solving for p_{X}, becomes:

$$p_{\mathrm{X}} = \frac{(N_{\mathrm{m}}+N_{\mathrm{f}})\,\varphi_{\mathrm{mf}}}{8\,N_{\mathrm{m}}\,N_{\mathrm{f}}-2N_{\mathrm{f}}(N_{\mathrm{m}}-1)\,\varphi_{\mathrm{mm}}-2N_{\mathrm{m}}(N_{\mathrm{f}}-1)\,\varphi_{\mathrm{ff}}-(4N_{\mathrm{m}}\,N_{\mathrm{f}}+N_{\mathrm{m}}+N_{\mathrm{f}})\varphi_{\mathrm{mf}}}. \qquad [\mathrm{A}5.18]$$

The consanguinity of a focal sex-i young adult to a random young adult of the same sex in their post-migration group is equal to the probability that neither migrated from their natal group multiplied by the consanguinity of individuals born in the same group, namely $p_{\mathrm{ii}} = (1 - m_{\mathrm{i}})^2\, p_{\mathrm{X}}$. Analogously, the consanguinity of the focal young adult to a random young adult of the opposite sex in their post-migration group is given by $p_{\mathrm{mf}} = p_{\mathrm{fm}} = (1 - m_{\mathrm{m}})(1 - m_{\mathrm{f}})\, p_{\mathrm{X}}$. Notice that these are independent from whether the group in which the two individuals were born were attack-first or defend-first groups.

The consanguinity of a focal young adult to a random adult of the same sex in their post-migration group is equal to the probability that the young adult did not migrate from their natal group multiplied by the consanguinity between an adult and a young adult in the same pre-migration group, namely $p_{\mathrm{m|EM}} = (1 - m_{\mathrm{m}})\, p_{\mathrm{born|EM}}$ or $p_{\mathrm{f|EF}} = (1 - m_{\mathrm{f}})\, p_{\mathrm{born|EF}}$. Analogously, the consanguinity of the focal young adult to a random adult of the opposite sex in their post-migration group is given by $p_{\mathrm{m|EF}} = (1 - m_{\mathrm{m}})\, p_{\mathrm{born|EF}}$ or $p_{\mathrm{f|EM}} = (1 - m_{\mathrm{f}})\, p_{\mathrm{born|EM}}$. Notice that these are independent from whether the group in which the two individuals were born were attack-first or defend-first groups.

The coefficient of relatedness between two individuals A and B, r_{AB}, is equal to the consanguinity of individual B to individual A, p_{AB}, divided by the consanguinity of individual B to themselves, $p_{\mathrm{BB}} = p_{\mathrm{self}}$ (Bulmer, 1994). The relatedness between a focal sex-i young adult and a random young adult of the same sex in their post-migration group is given by $r_{\mathrm{ii}} = p_{\mathrm{ii}}/p_{\mathrm{self}}$. Other coefficients of relatedness are derived analogously.

CONFLICTS OF INTEREST

At the beginning of the life cycle, in each group, adult men and women mate randomly and produce sons and daughters: these grow to become young adult men and women, while the adults become non-reproductive elder men and women (see Methods). There are thus four classes of individuals of interest in each group: young adult men, young adult women, elder men, and elder women.

Consider the case in which the trait $\mathcal{L}$ is controlled by a class of individuals within the attack-first group. Substituting consanguinities in condition [A5.9] with the appropriate consanguinities specified in Table A2.4.1 yields conditions for an increase in population average $\mathcal{L}$, when the trait is controlled by young adult men, young adult women, elder men, or elder women in the attack-first group. Setting the left-hand side of condition [A5.9] (that is, marginal fitness) to zero and evaluating at population average $\mathcal{L} = \mathcal{L}' = \bar{\mathcal{L}}$ (and thus $\lambda' = \bar{\lambda}$) gives the condition under which the controller is indifferent as to the probability of alliance formation. This is given by:

$$\frac{\frac{\partial \widetilde{W}_{\mathrm{f,att}}}{\partial \lambda}\Big|_{\mathcal{L}=\mathcal{L}'=\bar{\mathcal{L}}}}{\frac{\partial \widetilde{W}_{\mathrm{m,att}}}{\partial \lambda}\Big|_{\mathcal{L}=\mathcal{L}'=\bar{\mathcal{L}}}} = -v \qquad \text{[A5.19]}$$

where $v = p_{\mathrm{m|A}}/p_{\mathrm{f|A}} = (1 - m_{\mathrm{m}})/(1 - m_{\mathrm{f}})$ independently of the identity of the controller. This means that there is no conflict over alliance formation between young adult men, young adult women, elder men, and elder women within the attacking group.

Consider now the case in which the trait $\mathcal{L}$ is controlled by a class of individuals within the defeated group. Substituting consanguinities in condition [A5.12] with the appropriate consanguinities specified in Table A1 yields conditions for an increase in population average $\mathcal{L}$, when the trait is controlled by young adult men, young adult women, elder men, or elder women. Analogously to the previous case, setting the left-hand side of condition [A5.12] (that is, marginal fitness) to zero and evaluating at population average $\mathcal{L} = \mathcal{L}' = \bar{\mathcal{L}}$ (and thus $\lambda' = \bar{\lambda}$) gives the condition under which the controller is indifferent as to the probability of alliance formation. This is equal to:

$$\frac{\frac{\partial \widetilde{W}_{\mathrm{f,def}}}{\partial \lambda}\Big|_{\mathcal{L}=\mathcal{L}'=\bar{\mathcal{L}}}}{\frac{\partial \widetilde{W}_{\mathrm{m,def}}}{\partial \lambda}\Big|_{\mathcal{L}=\mathcal{L}'=\bar{\mathcal{L}}}} = -v \qquad \text{[A5.20]}$$

independently of the identity of the controller. Once again, analogously to the previous case, this means that there is no conflict over alliance formation between young adult men, young adult women, elder men, and elder women within the defending group.

Table A5.1 – Coefficients of consanguinity to be substituted in the general condition for increase in population average L to obtain conditions under the control of different classes of individuals in attack-first or defend-first groups.

	Attack-first group				**Defend-first group**			
Unspecified controller	**Young Men**	**Young Women**	**Elder Men**	**Elder Women**	**Young Men**	**Young Women**	**Elder Men**	**Elder Women**
$p_{\mathrm{m,att}\mid\mathrm{A}}$	p_{mm}	p_{mf}	$p_{\mathrm{m}\mid\mathrm{EM}}$	$p_{\mathrm{m}\mid\mathrm{EF}}$	-	-	-	-
$p_{\mathrm{f,att}\mid\mathrm{A}}$	p_{mf}	p_{ff}	$p_{\mathrm{f}\mid\mathrm{EM}}$	$p_{\mathrm{f}\mid\mathrm{EF}}$	-	-	-	-
$p_{\mathrm{m,def}\mid\mathrm{A}}$	-	-	-	-	p_{mm}	p_{mf}	$p_{\mathrm{m}\mid\mathrm{EM}}$	$p_{\mathrm{m}\mid\mathrm{EF}}$
$p_{\mathrm{f,def}\mid\mathrm{A}}$	-	-	-	-	p_{mf}	p_{ff}	$p_{\mathrm{f}\mid\mathrm{EM}}$	$p_{\mathrm{f}\mid\mathrm{EF}}$

We now consider conflicts of interest between a conquering and a defeated group over the tribute. The overall tribute ceded by the defeated group to the conquering group is given by $T = \tau_{\mathrm{m}} + \tau_{\mathrm{f}}\, v$. Notice that multiple configurations of male and female tribute may obtain the same overall tribute. For example, in a society in which women generally move to the husband’s group at marriage (patrilocality or female-biased dispersal, $m_{\mathrm{f}} > m_{\mathrm{m}}$), a randomly-chosen individual will on average be more related to the men than to the women in their group and will therefore value the reproductive success of women less than men’s (relative value, $v < 1$). In this case, a higher female tribute than male tribute will be required to obtain a given value of overall tribute. If, for instance, all men remain in their groups and three quarters of the women migrate at marriage ($m_{\mathrm{m}} = 0$; $m_{\mathrm{f}} = 3/4$; $v = 1/4$), one unit of male tribute carries the same weight of four units of female tribute.

Condition [5.1] in Results may be rearranged to obtain $T > T_{\mathrm{conq}}$, where $T_{\mathrm{conq}} = S(1 - B_{\mathrm{conq}})$ is the tribute value for which the conquerors are indifferent as to whether an alliance is formed, meaning that any tribute greater than this results in them favouring the alliance (for this reason and for simplicity, in Results, we term this value ‘minimum tolerated tribute threshold level’ for the conquering group). Analogously, condition [5.2] in Results may be rearranged to obtain $T < T_{\mathrm{def}}$, where $T_{\mathrm{def}} = S(1 - C_{\mathrm{def}})$ the tribute value for which the defeated are indifferent as to whether an alliance is formed, meaning that any tribute smaller than this results in them favouring the alliance (for this reason and for simplicity, in Results, we term this value ‘maximum tolerated tribute threshold level’ for the defeated group).

The minimum tolerated tribute threshold for the conquering group varies with war frequency, *a,* according to $\partial \mathrm{T}_{\mathrm{conq}} / \partial \mathrm{a} = -\Delta\omega\big(1 - 3\kappa a^2 \omega_{11} \bar{\lambda}\big) S$, which is negative for all allowed values of the parameters under consideration, meaning that an increase in *a* makes the condition for the formation of an alliance *less stringent.* On the other hand, the minimum tolerated tribute threshold for the defeated group varies with *a* according to $\partial \mathrm{T}_{\mathrm{def}} / \partial \mathrm{a} = -a\omega_{11}\kappa(2 - 3\mathrm{a}\Delta\bar{\lambda})S$, which is negative for $\Delta < 2/(3a\bar{\lambda})$ (which is verified, for example for $\omega_{11} = 1/2$), meaning that an increase in *a* makes the condition for the formation of an alliance *more stringent*.

The minimum tolerated tribute threshold for the conquering group varies with increase in probability of winning when having an ally, Δ, according to $\partial \mathrm{T}_{\mathrm{conq}} / \partial \Delta = -\mathrm{a}\big(1 - \kappa a^2 \omega_{11} \bar{\lambda}\big) S$, which is negative for all allowed values of the parameters under consideration, meaning that an increase in Δ makes the condition for the formation of an alliance *less stringent*. On the other hand, the maximum tolerated tribute threshold for the defeated group varies with Δ according to $\partial \mathrm{T}_{\mathrm{def}}/\ \partial \Delta = \kappa a^3 \omega_{11} \bar{\lambda} S$, which is positive for all allowed values of the parameters under consideration, meaning that an increase in Δ makes the condition for the formation of an alliance *less stringent*.

The minimum tolerated tribute threshold for the winning group varies with fatigue κ according to $\partial \mathrm{T}_{\mathrm{conq}}/\ \partial \kappa = \Delta a^3 \omega_{11} \bar{\lambda} S$, which is positive for all allowed values of the parameters under consideration, meaning that an increase in κ makes the condition for the formation of an alliance *more stringent*. On the other hand, the maximum tolerated tribute threshold for the defeated group varies with κ according to $\partial \mathrm{T}_{\mathrm{def}}/\ \partial \kappa = -a^2 \omega_{11}(1 - a\Delta\bar{\lambda})S$, which is negative for all allowed values of the parameters under consideration, meaning that an increase in a makes the condition for the formation of an alliance *more stringent*.

Second model: negotiations over tribute value (resolution)

We now model negotiations over tribute value between a conquering and a defeated group. We explore a simple illustrative case in which women do not have access to reproductive opportunities in defeated groups, thus focusing exclusively on the interests of men ($\sigma_{\mathrm{f}} = \tau_{\mathrm{f}} = 0$) (see also Methods).

FITNESS

The relative fitness of a randomly-chosen individual of unspecified sex is identical to the one given in the first model (equation [A5.2]). The absolute fitness of a focal young adult man in an attack-first group, is identical to the one derived for the first model (equation [A5.3]), with the exception of the first sub-phase in case (iii). Specifically, in this case, the focal young adult man competes for $\tau_{\mathrm{m}} N_{\mathrm{m}}$ breeding spots in the defeated group with $\tau_{\mathrm{m}}' N_{\mathrm{f}} K_{\mathrm{m}}$ young adult men from his group and $(1 - \tau_{\mathrm{m}}') N_{\mathrm{f}} K_{\mathrm{m}}$ from the defeated group, such that his probability of securing a breeding spot is $\tau_{\mathrm{m}} N_{\mathrm{m}} / (\tau_{\mathrm{m}}' N_{\mathrm{f}} K_{\mathrm{m}} + (1 - \tau_{\mathrm{m}}') N_{\mathrm{f}} K_{\mathrm{m}})$. That is:

$$
\begin{aligned}
w_{\mathrm{m,att}} = {} & (1 - a + a(1 - \omega_{11}))\left((1 - a + a(1 - \omega_{11})) + a\omega_{11}\left((1 - a^2\omega_{11}\bar{\lambda})(1 - \sigma_{\mathrm{m}}) + a^2\omega_{11}\bar{\lambda}(1 - (1 - \kappa)\sigma_{\mathrm{m}})\right)\right)\frac{N_{\mathrm{m}}}{N_{\mathrm{f}} K_{\mathrm{m}}} \\
& + a\omega_{11}(1 - \lambda)\left(\sigma_{\mathrm{m}} + (1 - a + a(1 - \omega_{11})) + a\omega_{11}\left((1 - a^2\omega_{11}\bar{\lambda})(1 - \sigma_{\mathrm{m}}) + a^2\omega_{11}\bar{\lambda}(1 - (1 - \kappa)\sigma_{\mathrm{m}})\right)\right)\frac{N_{\mathrm{m}}}{N_{\mathrm{f}} K_{\mathrm{m}}}
\end{aligned}
$$

$$+a\omega_{11}\lambda\left(\tau_{\mathrm{m}} + (1 - a + a(1 - \omega_{12})) + a\omega_{12}\left((1 - a^2\omega_{11}\bar{\lambda})(1 - \sigma_{\mathrm{m}}) + a^2\omega_{11}\bar{\lambda}(1 - (1 - \kappa)\sigma_{\mathrm{m}})\right)\right)\frac{N_{\mathrm{m}}}{N_{\mathrm{f}}K_{\mathrm{m}}} \tag{A5.21}$$

Considered that we assume $\sigma_{\mathrm{f}} = \tau_{\mathrm{f}} = 0$, the absolute fitness of a focal young adult woman in an attack-first group is given by:

$$\begin{aligned}
w_{\mathrm{f,att}} &= (1 - a + a(1 - \omega_{11}))\left((1 - a + a(1 - \omega_{11})) + a\omega_{11}\left((1 - a^2\omega_{11}\bar{\lambda}) + a^2\omega_{11}\bar{\lambda}\right)\right)\frac{N_{\mathrm{f}}}{N_{\mathrm{f}}K_{\mathrm{f}}} \\
&+a\omega_{11}(1 - \lambda)\left((1 - a + a(1 - \omega_{11})) + a\omega_{11}\left((1 - a^2\omega_{11}\bar{\lambda}) + a^2\omega_{11}\bar{\lambda}\right)\right)\frac{N_{\mathrm{f}}}{N_{\mathrm{f}}K_{\mathrm{f}}} \\
&+a\omega_{11}\lambda\left((1 - a + a(1 - \omega_{12})) + a\omega_{12}\left((1 - a^2\omega_{11}\bar{\lambda}) + a^2\omega_{11}\bar{\lambda}\right)\right)\frac{N_{\mathrm{f}}}{N_{\mathrm{f}}K_{\mathrm{f}}}
\end{aligned} \tag{A5.22}$$

Analogously, the absolute fitness of a focal young adult man in a defend-first group, is identical to the one derived for the battleground model (equation [A5.4]), with the exception of the first sub-phase in case (iii). Specifically, in this case, the focal young adult man competes for $(1 - \tau_{\mathrm{m}}')N_{\mathrm{m}}$ breeding spots in their group with $(1 - \tau_{\mathrm{m}}')N_{\mathrm{f}}K_{\mathrm{m}}$ young adult men from his group and $\tau_{\mathrm{m}}'N_{\mathrm{f}}K_{\mathrm{m}}$ from the attacking group, such that his probability of securing a breeding spot is $(1 - \tau_{\mathrm{m}}')N_{\mathrm{m}}/((1 - \tau_{\mathrm{m}}')N_{\mathrm{f}}K_{\mathrm{m}} + \tau_{\mathrm{m}}'N_{\mathrm{f}}K_{\mathrm{m}})$. That is:

$$\begin{aligned}
w_{\mathrm{m,def}} &= (1 - a + a(1 - \omega_{11}))\left(1 + a\left((1 - a^2\omega_{11}\bar{\lambda})\omega_{11}\sigma_{\mathrm{m}} + a^2\omega_{11}\bar{\lambda}\omega_{12}\sigma_{\mathrm{m}}\right)\right)\frac{N_{\mathrm{m}}}{N_{\mathrm{f}}K_{\mathrm{m}}} \\
&+a\omega_{11}(1 - \lambda)\left((1 - \sigma_{\mathrm{m}}) + a\left((1 - a^2\omega_{11}\bar{\lambda})\omega_{11}\sigma_{\mathrm{m}} + a^2\omega_{11}\bar{\lambda}\omega_{12}\sigma_{\mathrm{m}}\right)\right)\frac{N_{\mathrm{m}}}{N_{\mathrm{f}}K_{\mathrm{m}}} \\
&+a\omega_{11}\lambda\Bigg((1 - \tau_{\mathrm{m}}') + (1 - a)\left(a\left((1 - a^2\omega_{11}\bar{\lambda})\omega_{11}\sigma_{\mathrm{m}} + a^2\omega_{11}\bar{\lambda}\omega_{12}\sigma_{\mathrm{m}}\right)\right) \\
&\qquad + a\left(a\left((1 - a^2\omega_{11}\bar{\lambda})\omega_{11}(1 - \kappa)\sigma_{\mathrm{m}} + a^2\omega_{11}\bar{\lambda}\omega_{12}(1 - \kappa)\sigma_{\mathrm{m}}\right)\right)\Bigg)\frac{N_{\mathrm{m}}}{N_{\mathrm{f}}K_{\mathrm{m}}}
\end{aligned} \tag{A5.23}$$

Considered that we assume $\sigma_{\mathrm{f}} = \tau_{\mathrm{f}} = 0$, the absolute fitness of a focal young adult woman in a defend-first group is given by:

$$w_{\mathrm{f,def}} = (1 - a + a(1 - \omega_{11}))\frac{N_{\mathrm{f}}}{N_{\mathrm{f}}K_{\mathrm{f}}} + a\omega_{11}(1 - \lambda)\frac{N_{\mathrm{f}}}{N_{\mathrm{f}}K_{\mathrm{f}}} + a\omega_{11}\lambda\frac{N_{\mathrm{f}}}{N_{\mathrm{f}}K_{\mathrm{f}}} \tag{A5.24}$$

The sum of the average fitness for the attack-first and the defend first class for a given sex is $\bar{w}_{\mathrm{i,att}} + \bar{w}_{\mathrm{i,def}} = 2N_{\mathrm{i}}/(N_{\mathrm{f}}K_{\mathrm{i}})$. The tilde-fitness of a focal sex-i young adult who is part of a j-first group is given by $\widetilde{W}_{\mathrm{i,j}} = w_{\mathrm{i,j}}/(2N_{\mathrm{i}}/(N_{\mathrm{f}}K_{\mathrm{i}}))$, where i ∈{m,f} and j ∈{att,def}.

DIPLOMACY – MARGINAL FITNESS

Consider a locus $\mathcal{G}$, which controls a trait Λ, which is termed 'diplomacy' and is expressed by young adult men in attack-first groups. We denote the genic value of the focal individual for this gene by g, the breeding value of the controller by G, the breeding value of a groupmate's controller by G', and the population average breeding value by $\bar{G}$. Assuming vanishing genetic variation – all breeding values of the population are clustered around the mean (Taylor & Frank 1996, Frank 1997), the direction of natural selection is given by:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_{\mathrm{m}}\frac{\mathrm{d}\widetilde{W}_{\mathrm{m,att}}}{\mathrm{d}g_{\mathrm{m,att}}} + c_{\mathrm{m}}\frac{\mathrm{d}\widetilde{W}_{\mathrm{m,def}}}{\mathrm{d}g_{\mathrm{m,def}}} + c_{\mathrm{f}}\frac{\mathrm{d}\widetilde{W}_{\mathrm{f,att}}}{\mathrm{d}g_{\mathrm{f,att}}} + c_{\mathrm{f}}\frac{\mathrm{d}\widetilde{W}_{\mathrm{f,def}}}{\mathrm{d}g_{\mathrm{f,def}}} \qquad \text{[A5.25]}$$

The first derivative in equation [A5.25] describes the impact of the genic value of a gene drawn from a young adult man in an attack-first group on his tilde-fitness. Employing the chain rule, it can be expanded, obtaining:

$$\frac{\mathrm{d}\widetilde{W}_{\mathrm{m,att}}}{\mathrm{d}g_{\mathrm{m,att}}} = \frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\Lambda}\frac{\mathrm{d}\Lambda}{\mathrm{d}G}\frac{\mathrm{d}G}{\mathrm{d}g_{\mathrm{m,att}}} + \frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\Lambda'}\frac{\mathrm{d}\Lambda'}{\mathrm{d}G'}\frac{\mathrm{d}G'}{\mathrm{d}g_{\mathrm{m,att}}} = \left(\frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\Lambda}p_{\mathrm{m,att}|\mathcal{A}} + \frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\Lambda'}p_{\mathrm{m,att|A}}\right)\gamma \qquad \text{[A5.26]}$$

where $\partial\widetilde{W}_{\mathrm{m,att}}/\mathrm{d}\Lambda$ is the impact of the phenotype of the focal young adult man in an attack-first group on his tilde-fitness, $\partial\widetilde{W}_{\mathrm{m,att}}/\mathrm{d}\Lambda$ is the impact of the phenotype of a random young adult man in the focal attack-first group on the fitness of the focal young adult man in the same attack-first group, $p_{\mathrm{m,att}|\mathcal{A}} = \mathrm{d}G/\mathrm{d}g_{\mathrm{m,att}}$ is the consanguinity of the controller of the focal young adult man in the focal attack-first group (denoted by $\mathcal{A}$) to that focal young adult man, $p_{\mathrm{m,att|A}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{m,att}}$ is the consanguinity between the controller of a random young adult man in the focal attack-first group (denoted by A) to the focal young adult man, and $\gamma = \mathrm{d}\mathit{\Lambda}/\mathrm{d}G = \mathrm{d}\mathit{\Lambda}'/\mathrm{d}G'$ is the correlation between an individual's phenotype and the breeding value of their controller.

The second derivative in equation [A5.25] describes the impact of the genic value of a gene drawn from a young adult man in a defend-first group on his tilde-fitness. This is null, as diplomacy is only expressed by young adult men in attack-first groups.

The third derivative in equation [A5.25] describes the impact of the genic value of a gene drawn from a young adult woman in an attack-first group on her tilde-fitness. Employing the chain rule, it can be expanded to reveal the indirect fitness component (there is no direct fitness component, as the phenotype is expressed by young adult men), obtaining:

$$\frac{\mathrm{d}\widetilde{W}_{\mathrm{f,att}}}{\mathrm{d}g_{\mathrm{f,att}}} = \frac{\partial\widetilde{W}_{\mathrm{f,att}}}{\partial\Lambda\prime}\frac{\mathrm{d}\Lambda\prime}{\mathrm{d}G\prime}\frac{\mathrm{d}G\prime}{\mathrm{d}g_{\mathrm{f,att}}} = \frac{\partial\widetilde{W}_{\mathrm{f,att}}}{\partial\lambda'}p_{\mathrm{f,att|A}}\gamma \qquad \text{[A5.27]}$$

where $\partial\widetilde{W}_{\mathrm{m,att}}/\mathrm{d}\Lambda'$ is the impact of the phenotype of a random young adult man in the focal attack-first group on the fitness of the focal young adult woman in the same attack-first group, and $p_{\mathrm{m,att|A}} = \mathrm{d}G'/\mathrm{d}g_{\mathrm{m,att}}$ is the consanguinity between the controller of a random young adult man in the focal attack-first group (denoted by A) to the focal young adult woman.

The fourth derivative in equation [A5.25] describes the impact of the genic value of a gene drawn from a young adult woman in a defend-first group on her tilde-fitness. This is null, as diplomacy is only expressed by young adult men in attack-first groups.

We consider that the tribute demanded by the focal man τ is a decreasing function of his diplomacy $\mathit{\Lambda}$, the tribute demanded by a random man his group (that is, the tribute demanded by his group as whole) τ' is a decreasing function of the average level of diplomacy of the group $\mathit{\Lambda}'$, and the probability that the focal attack-first group forms an alliance in the first sub-phase of the life cycle λ is a decreasing function of the tribute demanded by the focal group τ' (see Methods). Therefore: $\partial\widetilde{W}_{\mathrm{m,att}}/\mathrm{d}\mathit{\Lambda} = (\partial\widetilde{W}_{\mathrm{m,att}}/$

$\mathrm{d}\tau)(\mathrm{d}\tau/\mathrm{d}\mathit{\Lambda})$, $\partial\widetilde{W}_{\mathrm{m,att}}/\mathrm{d}\mathit{\Lambda}' = (\partial\widetilde{W}_{\mathrm{m,att}}/\mathrm{d}\tau')(\mathrm{d}\tau'/\mathrm{d}\mathit{\Lambda}') + (\partial\widetilde{W}_{\mathrm{m,att}}/\mathrm{d}\lambda)(\partial\lambda/\mathrm{d}\tau')(\mathrm{d}\tau'/\mathrm{d}\mathit{\Lambda}')$, and $\partial\widetilde{W}_{\mathrm{f,att}}/\mathrm{d}\mathit{\Lambda}' = (\partial\widetilde{W}_{\mathrm{f,att}}/\mathrm{d}\lambda)(\partial\lambda/\mathrm{d}\tau')(\mathrm{d}\tau'/\mathrm{d}\mathit{\Lambda}')$, where $-(\mathrm{d}\tau/\mathrm{d}\mathit{\Lambda}) = -(\mathrm{d}\tau'/\mathrm{d}\mathit{\Lambda}') = \mathrm{c}$ and $(-(\mathrm{d}\tau'/\mathrm{d}\mathit{\Lambda}'))(-(\partial\lambda/\mathrm{d}\tau')) = \mathrm{d}\lambda'/\mathrm{d}\mathit{\Lambda}' = b$. Substituting these expressions into equation [A5.25] we obtain:

$$\frac{\mathrm{d}W}{\mathrm{d}g} = c_{\mathrm{m}}\left(-\frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\tau}c\, p_{\mathrm{m,att|}\mathcal{A}} + \left(-\frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\tau'}c + \frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\lambda}b\right)p_{\mathrm{m,att|A}}\right)\gamma + c_{\mathrm{f}}\frac{\partial\widetilde{W}_{\mathrm{m,att}}}{\partial\Lambda'}p_{\mathrm{m,att|A}}\gamma \qquad [\mathrm{A5.28}]$$

The condition for an increase in population average $\mathit{\Lambda}$ is $\mathrm{d}W/\mathrm{d}g > 0$. Considering that $c_{\mathrm{f}} = c_{\mathrm{m}} = 1/2$ under diploid inheritance, this condition is given by:

$$-\bar{\lambda}\sigma_{\mathrm{m}}c\, p_{\mathrm{m,att|}\mathcal{A}} + \left(-(\sigma_{\mathrm{m}} - \bar{\tau}_{\mathrm{m}}) + a\Delta\left(1 - a^2\omega_{11}\bar{\lambda} + (1-\kappa)a^2\omega_{11}\bar{\lambda}\right)\sigma_{\mathrm{m}}\right)b\, p_{\mathrm{m,att|A}} > 0 \qquad [\mathrm{A5.29}]$$

Considering that every young adult man's diplomacy is controlled by himself, and dividing by p_{self} to obtain $p_{\mathrm{m,conq|}\mathcal{A}}/p_{\mathrm{self}} = \mathrm{r}_{\mathrm{self}} = 1$ and $p_{\mathrm{m,conq|A}}/p_{\mathrm{self}} = r_{\mathrm{mm}}$ (see CONSANGUINITY AND RELATEDNESS) and rearranging terms yields condition [5.4] in Results (diplomacy under individual control), where $T = \bar{\tau}_{\mathrm{m}}$.

Considering instead that every young adult man's diplomacy is controlled by his group as a whole (i.e. $\mathcal{A}$=A=group), and dividing by p_{self} to obtain $p_{\mathrm{m,conq|}\mathcal{A}}/p_{\mathrm{self}} = p_{\mathrm{m,conq|A}}/p_{\mathrm{self}} = p_{\mathrm{m,conq|group}}/p_{\mathrm{self}} = \mathrm{r}_{\mathrm{group}}$ and $p_{\mathrm{m,conq|A}}/p_{\mathrm{self}} = p_{\mathrm{m,conq|group}}/p_{\mathrm{self}} = r_{\mathrm{group}}$ and rearranging terms yields condition [5.3] in Results (diplomacy under group control). Notice that, being the two terms weighted by the same coefficient of relatedness, the latter cancel out and do not appear in condition [5.3] in Results.

CONFLICTS OF INTEREST

The marginal fitness for diplomacy when this is under the control of the individual young adult man is given by $\theta_{\mathrm{ind}} = -\bar{\lambda}\, c + \left(-S + T + B_{\mathrm{conq}}\, S\right)b\; r_{\mathrm{mm}}$ (i.e. equal to the left-hand side of condition [5.4] in Results). The marginal fitness for diplomacy when this is under the control of the group is instead given by $\theta_{\mathrm{group}} = -\bar{\lambda}\, c + \left(-S + T + B_{\mathrm{conq}}\, S\right)b$ (i.e.

equal to the left-hand side of condition [5.3] in Results). Considered that $0 \leq r_{\mathrm{mm}} \leq 1$, it follows that $\theta_{\mathrm{ind}} \leq \theta_{\mathrm{group}}$, which implies $\Lambda^*_{\mathrm{ind}} \leq \Lambda^*_{\mathrm{group}}$. That is, the level of diplomacy predicted to evolve under individual control is always equal or lower than that expected to evolve under group control – meaning that there is conflict within the conquering group, between group interests and individual interests.

In addition, the level of diplomacy predicted to evolve under individual control is a decreasing function of the rate of male migration m_{m} and group size, i.e. the number of male and female breeding spots N_{m} and N_{f} (through their impact on relatedness coefficient r_{mm}; see CONSANGUINITY AND RELATEDNESS). In contrast, the level of diplomacy predicted to evolve under group control is independent of these parameters

ILLUSTRATIONS

For the purposes of illustration alone (see Fig. 5.2), we make the probability function of alliance formation λ explicit. Notice that the results of the second model (and especially conditions [5.3] and [5.4] and the conflict between group and individual interests) do not hinge on any particular functionalization. We consider that the probability than an alliance between a conquering group and a defeated group is formed, λ, is a sigmoidal function of the tribute demanded by the conquering group T and the maximum tolerated tribute threshold for the defeated group (T_{def}, calculated from the first model) – specifically $\lambda = 1/(1 + e^{-(T_{\mathrm{def}}-T)/\epsilon})$, where ϵ controls the steepness of the curve. Notice that if $T > T_{\mathrm{def}}$ then $\lambda < 0.5$, whereas if $T < T_{\mathrm{def}}$ then $\lambda > 0.5$.

6 Discussion

> There is no reason to see a “deep roots” view of warfare as pernicious, fatalistic or pessimistic. All manner of undesirable things have deep roots, and yet can be remedied by advancing our understanding of them.
>
> –Luke Glowacki, Michael L. Wilson
> & Richard W. Wrangham (2017)

The aim of this thesis has been to employ evolutionary modelling to assess the potential for differences in incentives to influence or perform behaviours exhibited by parties at various levels of the biological organisation – genes, individuals, groups – in the context of human intergroup warfare. I have performed this theoretical exploration by tackling specific questions within this theme, analysing behaviours and situations in which the interests of different parties could potentially differ. In all cases, my aim has been to formalise and thus asses the logical status of suggestions in the literature regarding possible incentive asymmetries – and uncover potential new drivers. To achieve these goals, I have used a modelling framework obtained by reformulating and expanding a model by Lehmann and

Feldman (2008) based on kin selection theory (Hamilton, 1964), adapted each time to the specific question under consideration.

In the preceding four chapters, I have uncovered several instances of conflicts of interest within and between levels of the biological organisation and sex differences in behaviour. Moreover, I have revealed how, in some cases, these asymmetries in incentives can be driven by sex-biases in demography and, in others, by interactions and evolutionary feedbacks between the behaviour of different classes of individuals. A summary of the questions considered in these chapters and the answers obtained through these analyses are provided in Table 6.1.

Each research chapter is complete with its own introduction to the specific questions tackled in it and discussion of the results obtained. For this reason, in the present chapter, I provide a general discussion for the work developed in the thesis as a whole. That is, I explore how the analyses presented in Chapters 2-5 illuminate the theme of potential for asymmetries in incentives between various parties in human populations experiencing warfare. I place these results in the context of the relevant literature, establish links between the results of different chapters, and suggest avenues for future empirical testing and further theoretical exploration. I then reflect on the role of culture in explaining warfare and how my results may help illuminate this issue. I conclude by discussing the wider societal significance of the work presented here and the evolutionary study of human warfare more in general.

Table 6.1 – Summary of the questions addressed in Ch.2-5 and the answers provided by the analyses therein.

Questions & Answers	Ch.
Can intergroup aggression influence the evolution of sex-biased dispersal? Yes, the 'ecology of warfare' can drive the evolution of sex biases in dispersal. In particular, my analysis shows that if, as a result of victory in warfare, women do not obtain additional reproductive opportunities but men do (as it seems to be the case in numerous small-scale societies), then women are favoured by natural selection to disperse at a higher rate than men, resulting overall in female-biased dispersal.	2
Is there potential for parent-offspring conflicts over belligerence and bravery? Their drivers? Yes, my analysis predicts that parents and their son are always in conflict over the level of belligerence and bravery that young adult males should show. Parents favour a higher level than their son does, because they are more related to their son's groupmates than he is.	2
Is there potential for sexual conflicts over belligerence and bravery? Their drivers? Yes, my analysis reveals that there is potential for conflicts between mothers and fathers, whenever there are asymmetries in relatedness between the sexes. If, on average, adult men are more related to their sons' groupmates than adult women are – as a result of female-biased dispersal, for example – then fathers favour a higher level of belligerence and bravery in their sons than mothers do. The opposite pattern is expected when women are more related to young adults in the group than men are, for example as a result of male-biased dispersal.	2
Is there potential for intragenomic conflicts over belligerence and bravery? Their drivers? Yes, my analysis reveals that there is potential for conflict between the warrior's own paternal-origin and maternal-origin genes, driven by asymmetries in relatedness to young adult males in the group, analogous to those generating sexual conflict.	2
What are the consequences of these intragenomic conflicts? My analysis suggests that these conflicts can lead to the evolution of genomic imprinting, i.e. parent-of-origin-specific gene expression. This can lead to the emergence of behavioural disorders through mutations and epimutations.	2
Existing hypotheses suggest that sex differences have driven the evolution of almost-exclusively male participation in warfare. Are these differences necessary? No, they are not. My analysis reveals that an evolutionary feedback between male participation in war and female participation in war can drive the evolution of exclusively-male warfare even in the absence of any other sex difference – the only conditions being an initial male bias in participation and decelerating costs of warfare. The sex biases previously explored in the literature merely make this outcome more likely.	3
Can intergroup aggression influence which sex performs altruism towards groupmates? Does the sex of the recipients matter? Yes, my analysis suggests that sex is a fundamental modulator of altruistic behaviours in populations experiencing warfare. Firstly, all else being equal, the more philopatric sex is favoured to be more altruistic towards same-sex than opposite-sex groupmates. Secondly, all else being equal, the sex for which competition for reproductive opportunities is relatively more global is favoured to be more altruistic towards same-sex than opposite-sex groupmates. Furthermore, these two factors can reinforce each other or act in opposite directions, with different combinations of dispersal and admixture leading to different patterns of altruism.	4
Is there potential for conflicts of interest between a victorious and a defeated group over alliance formation? Yes, for a given value of tribute to be ceded by the defeated group to the conquering group, the two groups may disagree as whether to form an alliance.	5
Is there potential for conflicts of interest within the victorious group over alliance formation? Yes, single individual conquerors and the conquering group as a whole are in conflict over levels of diplomacy and thus the extent of tribute to be demanded. The group as a whole favours a lower request, which results in a greater probability of alliance formation	5

Asymmetries in incentives: drivers

Overall, the work developed in this thesis suggests that there is considerable scope for differences in incentives – to perform or influence behaviours – to arise in the context of human warfare. The analyses that I have performed have shown that such asymmetries can result from differences in demographic parameters between parties (demography) and/or can arise in response to the behaviours performed by other individuals (evolutionary feedbacks and hysteresis effects). Moreover, they have highlighted that such differences in incentives can become manifest in two ways: conflicts of interest and behavioural differences. I discuss these two drivers and two manifestations in the context of the relevant literature.

Demography

Taken together, the analyses performed in this thesis suggest that demography is often a crucial driver of incentive differences to perform or influence behaviours observed in the context of war. In this thesis, I have: a) clarified the role of dispersal and the genetic mixing resulting from movement of individuals as a consequence of victory and defeat (admixture); b) explored how biases in these demographic parameters can lead to incentive differences between various classes of individuals; c) shown that, not only does demography influence war, but the 'ecology of warfare' can in turn contribute to shaping demographic patterns. Point c) was discussed in Chapter 2. Here, I discuss points a) and b).

Limited dispersal was first suggested as a mechanism for the evolution of within-group altruism – even in the absence of kin recognition – by Hamilton (1964). Taylor (1992) explored this question with an analytical kin-selection model. Surprisingly, he showed that – in the simplest possible case of a large population subdivided into groups connected by random migration – limited dispersal did not result in within-group altruism being favoured by natural selection. This was because limited dispersal led, at the same time, to an increase in the inclusive fitness benefits associated with altruism – as recipients were more highly related to the actor – and to an increase in competition between kin, with a consequent inclusive fitness cost. Taylor (1992) showed that these two effects, the costs and the benefit, exactly cancelled out (notice that Frank (1985, 1986a, 1986b) and Bulmer (1986), had reached a similar conclusion in the context of sex ratio determination, an altruistic trait). In almost three decades since the publication of this seminal work, several researchers have attempted to identify ways in which limited dispersal can indeed lead to increased altruism. These consist in cases in which the fitness enhancing effect of limited dispersal can be decoupled from an increase in kin competition and include, among others, dispersal in buds (Gardner and West, 2006; Lehmann, et al., 2006), overlapping generations (Taylor and Irwin, 2000; Irwin and Taylor, 2001), and sex structure (Johnstone and Cant, 2008; Gardner, 2010) (see Lehmann and Rousset, 2010, for a recent and extensive review of the topic).

Lehmann and Feldman's (2008) kin selection model of intergroup aggression showed that warfare could provide one such avenue. By being belligerent or brave, individual young adult males increase the chances that their groupmates obtain a breeding position in another group (that is, the defeated group) rather than the home group. In this way, lower rates of dispersal increase the inclusive fitness returns of belligerence and bravery, without increasing competition between kin in the home group. In this thesis, and specifically in Chapter 4, I have shown that the presence of intergroup warfare provides a way to decouple the effects of limited dispersal for altruism in general – i.e. any behaviour that decreases the competitiveness of the actor and increases that of the recipient (Hamilton, 1964) – not just belligerence and bravery.

In my analysis of the evolution of altruism in a population experiencing warfare, I have shown that individuals are favoured to be altruistic towards other group members insofar as the help provided leads to increased chances of obtaining reproductive opportunities in a group other than the home group. This scenario is made possible by the conquest of breeding spots in other groups as a consequence of war. Specifically, the incentive to perform altruistic behaviours depends on the admixture resulting from conquest. For example, scenarios in which half of the conquered group breeding spots are seized by the attackers and the rest are left to the defeated (s=0.5, M=0.25) lead to the highest levels of altruism, as kin competition is lowest in this case.

In addition to clarifying the role of dispersal and admixture in the context of warfare, the work in this thesis has explored the consequences of sex differences in these two demographic parameters. In the setup of their model, Lehmann and Feldman (2008) allowed for sex specific demography, with rates of dispersal and fractions of breeding spots obtained in conquered groups being potentially different for men and women. However, in their analysis, they assumed equal dispersal rates for the two sexes ($m_m=m_f=m$), preventing the consideration of potential consequences of differences between the sexes in this respect.

In the analyses in Chapters 2-4, I have explored both the case in which dispersal is female-biased ($m_m<m_f$) and the case in which dispersal is male-biased ($m_m>m_f$). I have shown that such biases can lead to several instances of conflicts of interest over warfare-related altruistic behaviours (see also discussion in the *Conflicts of interest* section below).

I have provided expected patterns of warfare-related behaviours (belligerence and bravery) and within-group altruism under different ancestral patterns of dispersal, female-biased and male-biased. But what timescale is needed for a given pattern of dispersal to result in the evolution of differences in incentives between parties? To my knowledge, clear estimates for these timescales are not available. Therefore, two scenarios are possible. I explore them in turn.

The first is that these dispersal patterns need to have been present for very long periods of time – e.g. tens or hundreds of thousands of years – to result in behavioural differences. In this case, we would expect a relative homogeneity in current human populations with respect to the expression (or parental preference) of the traits under consideration – as these would have been shaped by our Pleistocene ecology, after our lineage separated from the one leading to modern *Pan* species (cf. Foley, 1995). Dispersal patterns during this very long period are highly debated and a consensus has not been reached yet (see Box 6.1). If, as some lines of evidence seem to suggest (Ember 1975, 1978; Manson and Wrangham, 1991; Seielstad, et al., 1998; Chapais, 2008), female-biased dispersal was dominant, then we would expect the patterns of expressions indicated under this dispersal regime in Chapters 2-4.

If instead, as others suggest (Marlowe, 2004; Wilkins and Marlowe, 2006; Hill, et al., 2011; Sugiyama, 2017), there was no sex bias in dispersal in ancestral human populations, then – with respect to the dispersal factor alone – we would expect no differences in parental preference for belligerence or bravery, no intragenomic conflicts over these traits, and no sex differences in altruism. However, it is important to underline that there are other factors – not directly investigated in this thesis – that can generate relatedness asymmetries.

For example, higher male variance in reproductive success (perhaps associated with polygynous mating) results in higher relatedness through fathers than through mothers (cf. Úbeda and Gardner, 2010). Thus, this would be expected to lead fathers to encourage their sons to expend effort in warfare more than mothers, and to intragenomic conflicts in which paternal-origin genes favour higher expression – generating expression patterns analogous to those suggested here for female-biased dispersal (cf. Ch.2, Fig. 2.2-4).

The second possibility is that shorter periods of time – e.g. in the order of millennia – are enough for selection to generate these differences. In this case, we would expect to find variation in the behaviours discussed in this thesis across human populations – associated with dispersal patterns. Dispersal of men and women is mediated by residence rules in human societies, that is cultural norms that prescribe where a newly-wed couple should live (Jordan, et al., 2009; see Box 6.2). Therefore, we would expect patrilocal societies, in which a woman moves to the husband's household at marriage, to show the patterns predicted for female-biased dispersal. On the other hand, we would expect matrilocal societies, in which it is the man who moves to the spouse's household, to show patterns predicted for male-biased dispersal. For example, we would expect patrilocal and matrilocal populations to show different patterns of genomic imprinting and gene expression of the belligerence and bravery genes investigated in Chapter 2 (see Fig.6.1 for a summary of expected patterns under the two dispersal regimes).

These behavioural predictions for belligerence/bravery (Ch.2) and for altruism (Ch.4) would ideally be tested in societies within a language group that diverged from a single population in the last few millennia and that share similar ecology, but now differ in residence rules. Austronesian-speaking and Bantu-speaking groups seem especially promising, as the evolution of residence norms in these two lineages has recently been illuminated using cultural phylogenetic analyses (Jordan, et al., 2009; Opie, et al., 2014). These methods use language phylogenies and information about current states – of a cultural practice or rule – to reconstruct past states, analogously to what is done for species phylogenies (Mace and Pagel, 1994; Mace and Holden, 2005; Gray, et al., 2007). Both Austronesian and Bantu groups now present a variety of residence norms (with matrilocal, patrilocal, and ambilocal societies) but the former were ancestrally matrilocal (Jordan, et al, 2009; see also Hage and Marck, 2003; Kayser, et al., 2008; Fortunato and Jordan, 2010) and the latter were ancestrally patrilocal (Opie, et al., 2014). Questionnaires evaluating views on warfare and bravery could be used in cases of societies that have been pacified as a result of colonialism and/or State policing.

Finally, it is important to highlight that the work presented in this thesis, especially in Chapter 2, 3 and 4, also constitutes a contribution to the development of parochial altruism theory. This framework suggests that within-group altruism and between-group aggression have been tightly linked throughout human evolution (Choi and Bowles, 2007; Bowles, 2009). In his recent and extensive review of the topic, Rusch (2014) highlighted the need to further develop the theory to consider the potential for sex differences in warfare and altruistic behaviours – as current models abstract away sexual reproduction for mathematical tractability. In this thesis, I have offered a contribution in this direction, showing that the two sexes can be in conflict over warfare behaviours, resulting in only one sex participating in warfare and members of the two sexes exhibiting different levels of altruism as a result of intergroup conflict.

Box 6.1 – Sex-specific dispersal in ancestral humans

There is great controversy surrounding the question as to whether the rates of male dispersal and female dispersal differed in ancestral human populations, living a hunter-gatherer lifestyle in the Pleistocene (Marlowe, 2004; Wilkins and Marlowe, 2006; Sugiyama, 2017). Three research avenues can help illuminate this issue.

The first is the study of dispersal patterns in extant great apes (hominids). Chimpanzees and bonobos, our closest living relatives are characterised by female-biased dispersal, as are gorillas (Lawson Handley and Perrin, 2007). This suggests that ancestral humans might have followed this pattern too (e.g. Manson and Wrangham, 1991; Chapais, 2008; but see Sugiyama, 2017).

The second line of evidence comes from population genetics studies that estimate patterns of dispersal in our past by examining variation in mitochondrial DNA (which is maternally inherited) and the non-recombining region of the Y-chromosome (which is paternally inherited). The first such analysis (Seielstad, et al., 1998) found evidence of higher female dispersal, but a successive one (Wilder, et al., 2004) did not confirm this result. Wilkins and Marlowe (2006) argue that the difference in the results of the two studies stems from a difference in the sampling scheme adopted. They suggest that the study by Wilder, et al. (2004), which identifies no bias, is more reflective of pre-agricultural societies, while the Seielstad, et al. (1998) study, which finds evidence of female-biased dispersal, captures residential patterns that emerged after the rise of agriculture.

Finally, the third line of evidence comes from the study of extant hunter-gatherers, which are considered the best available models for the lifestyle of ancestral humans (Marlowe, 2005). The majority of hunter-gatherer societies have long been considered to be characterised by patrilocal residence (Ember, 1975, 1978; Foley, 1995). However, recent work has questioned this. Individuals in hunter-gatherer societies move frequently between bands and spouses can move to either the husband’s or the wife’s band: for this reason, hunter-gatherers are best described as ‘multilocal’ or ‘bilocal’ (Marlowe, 2004; Hill, et al., 2011). However, this does not mean that dispersal is necessarily unbiased. For example, in a study of 32 extant hunter-gather societies, Hill, et al. (2011) find that in 17 societies there are more co-residing brothers than co-residing sisters, while only three show the opposite pattern, and the remaining 12 show no detectable bias.

Overall, notwithstanding the great developments in these three research avenues, it is still unclear what pattern of dispersal was followed by our Pleistocene ancestors. It is possible that dispersal has been female-biased throughout our history (becoming more pronounced with the advent of agriculture). Alternatively, it may have been unbiased during the Pleistocene and became female-biased – in association with patrilocal residence rules – after the agricultural evolution.

Box 6.2 – Sex-biased dispersal and post-marital residence systems

Sex-biases in dispersal – or lack thereof – in human populations are mediated by cultural norms termed post-marital residence rules which regulate the movement of spouses at marriage (Jordan, et al., 2009; Fortunato and Jordan, 2010). Systems can be divided in four broad categories: patrilocality, matrilocality, ambilocality, neolocality. In patrilocal societies, the wife moves to the husband's social group. About 70% of extant human societies follow this pattern (*Ethnographic Atlas*, Murdock, 1967; accessed using *D-PLACE*, Kirby, et al., 2016) and include, for example, the majority of Indo-European societies (Fortunato and Jordan, 2010) and numerous Bantu-speaking groups (Opie, et al, 2014). In matrilocal societies, it is instead the husband who moves to the wife's social group at marriage. This system is practiced by a significant minority of societies worldwide (about 15%), including for example many Austronesian societies (Jordan, et al., 2009). In ambilocal societies, the newly-wed couple can decide where to reside (about 6%). This is the case for many hunter-gatherers, where residence is changed multiple times during life (Marlowe, 2004; Hill, et al., 2011). In neolocal societies, the couple founds a new household, which can be far away from the social groups of either spouse (about 5%). This is the dominant system in contemporary Western industrialised societies. Lastly, the rarest system (about 0.6%) is 'duolocality' or 'natolocality' where mating partner do not live together, but reside in the natal household, and the man visit the woman at night ('walking marriage'). This system is practiced, for example, by the Mosuo of South-Western China (Cai, 2001; Wu, et al, 2013).

What do post-marital residence rules tell us about patterns of sex-biased dispersal of the societies that practice them? It is generally assumed that patrilocality results in female-biased dispersal, matrilocality results in male-biased dispersal, and ambilocality, neolocality, and duolocality in unbiased dispersal (e.g. Marlowe, 2004; Jordan, et al, 2009). However, it important to underline that it is not always clear what is meant by one spouse moving to the other's 'social group'. In some cases, this can mean band or village (that is, a multi-family group), and in others household or family within a village/band. This is important because if, for instance, wives generally move to the husband’s village this results in them being less related to the village inhabitants than the husband is. On the other hand, if movement occurs between households, both spouses would be equally related to the village. I believe that this issue needs to be clarified to allow a constructive interaction between evolutionary anthropology (which is often concerned with post-marital residence) and evolutionary biology (which is generally concerned with sex biases in dispersal). Mathematical modelling of populations with two levels of structure (village and household) could help in this respect.

A second important point that ought to be highlighted is that post-marital residence rules prescribe what individuals in a society should do. However, full compliance is rarely achieved (e.g. a study of Y chromosome variation by Raaum, et al. (2013) finds that, in Yemeni tribes, the patrilocal norm is not always respected). This means that sex-biases in dispersal resulting from post-marital residence rules may not be extreme (e.g patrilocality may not result in zero male dispersal and full female dispersal). This difficulty does not affect the results presented in this thesis as they are qualitative in nature: that is, I provide expected behavioural patterns under male-biased and female-biased dispersal, rather than making prediction for specific values of these parameters.

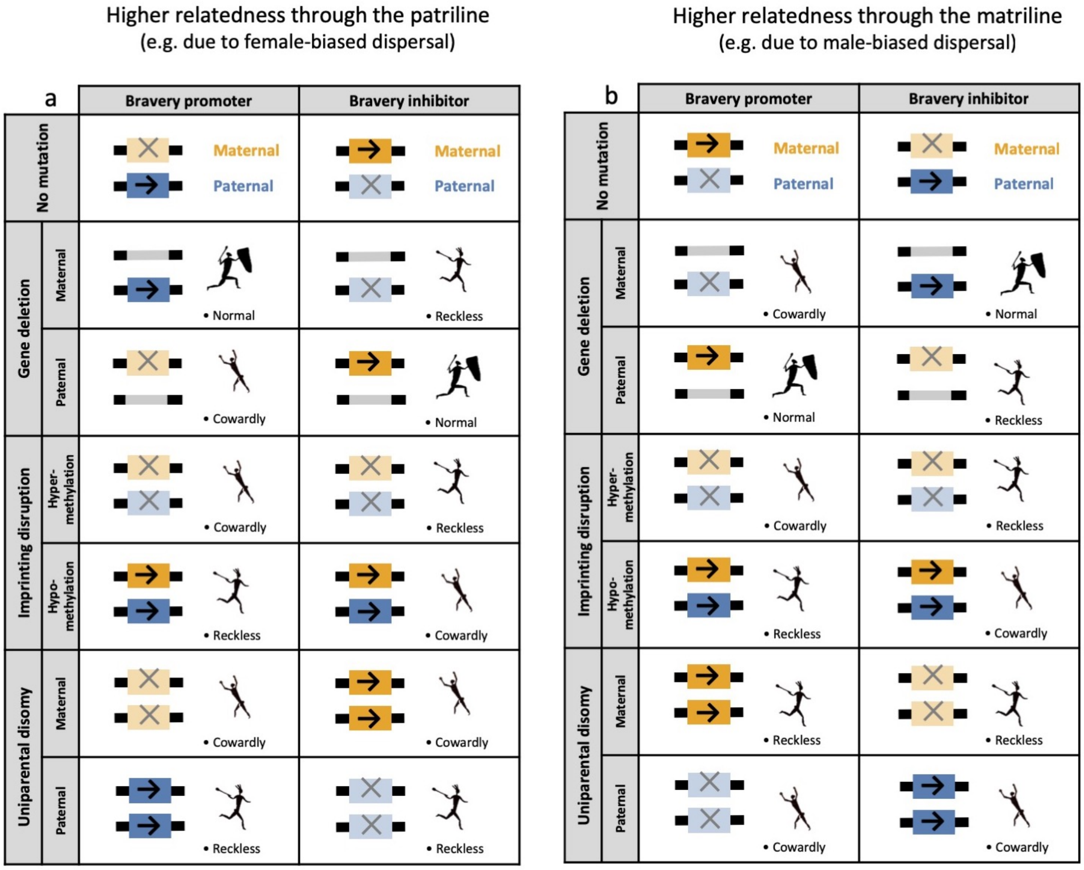

Figure 6.1 - Genomic imprinting of bravery loci and associated pathologies. Predicted patterns of parent-of-origin-specific gene expression and concomitant phenotypes for loci that are either promoters or inhibitors of bravery, under normal conditions and also as a result of three different mutational or epimutational perturbations (gene deletion, imprinting disruption, uniparental disomy) when relatedness is higher through the patriline (panel a) and when relatedness is higher through the matriline (panel b) Genes are either of maternal-origin (orange) or paternal-origin (blue), and are either silenced (crosses) or expressed (arrows). Human figures from the George Stow collection at Iziko South African Museum, derived from The Digital Bleek and Lloyd (http://lloydbleekcollection.cs.uct.ac.za/) with permission.

Feedbacks and hysteresis effects

The work in this thesis highlighted another possible driver of differences in incentives to perform or influence behaviours in the context of warfare: a party's incentive can depend on the current behaviour of another party, with the generation of evolutionary feedbacks between different parties. Such feedbacks can lead to non-trivial outcomes in terms of behavioural patterns and may result in dependence on initial conditions (hysteresis).

Specifically, in Chapter 3, I showed that fundamental differences between the sexes – including greater male effectiveness in warfare, lower costs for men, and higher female dispersal – are not necessary to explain the near-complete absence of women from the battlefield until very recent times. Instead, this pattern is generated by a feedback between participation of the two sexes: specifically, even in the absence of any other sex differences, participation by men relatively incentivises other men to join and relatively disincentivises women, so that any initial symmetry-breaking bias in participation becomes exaggerated in men-only participation.

It is possible that feedbacks analogous to those described in Chapter 3 could apply in the context of numerous other behaviours that could in principle be performed by both men and women. For example, in Chapter 4, I explored the evolution of sex-specific altruism in the context of war. For simplicity, I assumed that altruistic behaviours performed by men and women towards male and female groupmates did not influence each other and could be considered to evolve independently (see Chapter 4, Fig. 4.2). However, interactions between these behaviours could lead to evolutionary feedbacks analogous to those uncovered in Chapter 3. Further analysis, considering coevolutionary dynamics of different forms of altruism, is needed to explore this possibility.

Exploration of the potential for similar feedbacks could illuminate the evolution of other behavioural sex differences. For example, hunter-gatherer societies display sexual division of labour: men mainly cooperate to hunt high-risk high-reward prey, while women gather smaller food items, closer to camp (Lovejoy, 1981). Debate over the drivers of this pattern has witnessed a resurgence in the last couple of decades (Hawkes and Bliege Bird, 2002; Marlowe, 2007; Gurven and Hill, 2009). Supporters of the traditional view suggest that men and women are cooperating to support their offspring and sexual division of labour allows the achievement of this goal (Gurven and Hill, 2009). On the other hand, proponents of the 'signalling theory' suggest that hunting constitutes a way for men to honestly signal their quality as prospective mates (Hawkes and Bliege Bird, 2002). In either case – and even in the, perhaps likely, case in which both factors are at play – the puzzle remains as to why the sex difference in productive activities should be so extreme. Evolutionary feedbacks analogous to the ones explored in Chapter 3 could contribute to this pattern. In future, mathematical modelling could be developed to explore this possibility.

Asymmetries in incentives: manifestations

The first type of manifestations of incentive differences in the context of war which was highlighted by this thesis is constituted by conflicts of interest. These can be generated when the behaviours under consideration are performed only by a class of individuals or involve a decision at the group level – as is the case for belligerence and bravery, which influence war initiation and outcome (Ch.2), and for alliance-related behaviours (Ch.5).

I have shown that conflicts of interest over behaviours in the context of warfare can occur between multiple parties, both within and between levels of the biological organisation – genes, individuals, groups (Ch.2 and Ch.5). Starting from the lowest level of the organisation, I have shown that there is potential for conflict: a) between paternal-origin and maternal-origin genes within the same individual (over belligerence an bravery; Ch.2); b) between these genes and the individual who carries them (over belligerence an bravery; Ch.2); c) between this individual and his parents (over belligerence an bravery; Ch.2); d) between his father and his mother (over belligerence an bravery; Ch.2); e) between individual males and their group as a whole (over diplomacy and alliance formation with a defeated group; Ch,.5), f) between the interest of victorious group in war and the group they have defeated (over alliance formation, mediated by tribute value; Ch.5). Each of these conflicts was discussed in the context of the relevant literature in Chapters 2 and 5.

Another potential source of conflict that I have not considered in this thesis is age difference between individuals. Future research could explore how the evolutionary interests of an individual – with respect to behaviours in the context of war – changes with age. Theoretical work surrounding menopause has suggested that age can generate conflicts at multiple levels of the biological organisation with surprising outcomes (Cant and Johnstone, 2008; Johnstone and Cant, 2010; Úbeda, et al., 2014). Expansion of the model in this thesis to allow overlapping generations could potentially show conflicts analogous to those described above for menopause.

The second type of manifestations of incentive asymmetries highlighted in this thesis is constituted by behavioural sex differences. When different classes of individuals can perform a given behaviour (and each individual is in a position to decide at what level to exhibit such behaviour) asymmetries in incentives between classes of individuals can result in differences in behaviour. I have shown that these differences in behaviour can result in the case of participation in warfare (Ch.3) and of within-group altruism broadly defined (Ch.4), driven by demography, evolutionary feedbacks and their joint action (see previous section ‘Incentive asymmetries: drivers’).

Human societies are remarkable in that they present extremely high levels of cooperation, while exhibiting relatively widespread conflict within groups, between individuals and between constituent subgroups (Queller and Strassman, 2009). In this way they bear, in my opinion, some similarity to eusocial insect societies, such as honeybees (which present both ‘complexities of apparent purpose’ and ‘complexities of cross purpose’; Strassman and Queller, 2007). Given the extent of the conflicts, it is unlikely that our societies will ever achieve a major transition to an organismal-like level or superorganism (Stearns, 2007; Queller and Strassman, 2009; see also Gardner and Grafen, 2009 for a discussion of the term ‘superorganism’). However, this intermediate state between a loose group of individuals and a superorganism – this condition of being ‘stalled part way through a major evolutionary transition’ (Stearns, 2007, p.2275) – has generated the huge variation of human societies witnessed in the past and the present. Understanding how this occurred is a great challenge for human evolutionary research, with its multiple subdisciplines (Diamond, 1997; Stearns, 2007; Turchin, 2015). By exploring incentive asymmetries and conflicts of interest in the context of intergroup aggression, the work in this thesis has contributed to this effort, highlighting the complex interplay between cooperation and conflict.

The question of culture

Warfare, like the vast majority of human behaviours, is a complex phenomenon that cannot be accounted for by invoking a single factor, but is instead the result of the interaction of genetics, environment, proximate mechanisms and culture (Laland, et al., 2011; Glowacki, et al., 2017). Over the years, different researchers have focused on one or more of these different aspects – often following the guiding principles of the three main approaches in evolutionary anthropology, that is behavioural ecology, evolutionary psychology, cultural evolution (reviewed in Ch.1). While no-one denies the cultural phenomenon, the role of culture in explaining human warfare has been much debated with different scholars assigning differing degrees of importance to it.

Researchers close to the behavioural ecology and evolutionary biology traditions have conceptualised participation in warfare as a behaviour under strong genetic influence and with a long evolutionary history – going back at least to our last common ancestor with chimpanzees – that has evolved under genetic natural selection (Wrangham and Peterson, 1996; Wrangham and Glowacki, 2012; Glowacki and Wrangham, 2013, 2015; Wrangham, 2018). Theoretical work has help delineate how costly, altruistic warfare behaviours may be selected for thanks to their impact on inclusive fitness (Lehmann and Feldman, 2008; Lehmann, 2011). Evolutionary psychologists have taken a different approach and have suggested that warfare selected for different psychological adaptations in men and women that still influence intergroup conflict in the contemporary world, though they are, in many cases, no longer adaptive or even maladaptive ('male warrior hypothesis'; van Vugt, et al., 2006; van Vugt, 2009; McDonald, et al., 2012).

On the other hand, cultural evolutionists have suggested that explanations based on inclusive fitness and reciprocity – while enough to explain intergroup raiding by small groups – are not sufficient to explain large-scale warfare, which is uniquely human. Large-scale warfare occurs between entholinguistic groups: hundreds or thousands of unrelated individuals on each side take part to it, and the risk of mortality is high for both attackers and defenders (Zefferman and Mathew, 2015; Zefferman, et al., 2015). Cultural evolutionists suggest that this phenomenon is the result of 'group-structured cultural selection', also known as 'cultural group selection'. In this process, cultural transmission allows the build-up of behavioural differences between groups, making between-group selection stronger than within group selection and thus resulting in the evolution of cultural norms – such as participation in risky raids and battles – that favour the group while not necessarily maximising the fitness of the individual (Henrich, 2004; Turchin, et al., 2010 Zefferman and Mathew, 2015; Zefferman, et al., 2015; Richerson, et al., 2016). These norms also include sanctions for free riders, individuals that refuse to participate in warfare or do not expend sufficient effort (e.g. Turkana pastoralists in East Africa, Mathew and Boyd, 2011; Israel before and after the 2006 war with Hezbollah, Gneezy and Fessler, 2011).

Here, I have adopted a behavioural ecological approach to the question of warfare (cf. Ch.1, p18) and explored the inclusive fitness interests of various parties with respect to various warfare-related behaviours. Following Lehmann and Feldman (2008), I have modelled the traits under study as controlled by a single locus. I did so because this is the most efficient way to identify inclusive fitness interests, not because I believe that their genetic architecture is simple (cf. Ch.1, p.4 on the genetic basis of aggressive behaviours). I have not modelled cultural influence on warfare behaviours or cultural change as this was not the aim of this thesis. For this reason – while I do not deny that culture can influence warfare – I recognise that my research so far does not allow me to directly address the question of the relative importance of culture and genes. Similarly, it does not allow me to contribute to discussion surrounding the possibility that cultural processes may generate individual behaviours that are in conflict with individual inclusive fitness interests.

However, the work in this thesis has suggested a way in which inclusive fitness interests and culture may come to interact: culture can be an avenue for the inclusive fitness interests of a given party to prevail on those of other parties when there is conflict between these (see 'Asymmetries in incentives: manifestations' section). For example, I have shown that fathers disagree with their sons over the level of bravery they should show: fathers favour a higher level of bravery in their sons than their sons themselves do (Ch.2). Cultural transmission of knowledge about fighting techniques and weapon production might be an avenue for fathers to exert their influence on the warfare-related behaviours. As it is often fathers who pass on this knowledge (Goldschmidt, 1988), young adult males might be acting in the genetic interest of their fathers, not their own. Also, father-to-son transmission of knowledge might be a way for fathers to impose their interests more strongly than mothers – also because women do not participate in warfare. These predictions could be tested in the field, ideally in hunter-gatherer or other small-scale societies with hostile or violent interactions with neighbouring groups. Pastoralist groups in East Africa like the Turkana or the Nyangatom – who currently practice warfare and have recently been the focus of studies in the field (e.g. Mathew and Boyd, 2011; Glowacki and Wrangham, 2015) – would be appropriate systems.

A second example of how culture may become an avenue for the inclusive fitness interests of a given party to prevail over others was offered my study of alliance formation (Ch.5). Within-group conflicts between the interest of single individuals and the group as a whole can inhibit the formation of alliances and, in this way, the shift from small single-group societies to larger multi-group societies. Greater alignment between individual interests and group interests may be achieved through suppression of within-group competition (Alexander, 1979, 1987; Frank, 2003). Such suppression might be realised through cultural institutions, including laws whose function, according to Richard D. Alexander, was to 'regulate […] the reproductive strivings of individuals and subgroups within societies, in the *interest of* preserving unity in *the larger group*' (Alexander, 1979, p.240; emphasis my own). Exploration – through mathematical modelling – of possible mechanisms of suppression of competition though cultural institutions constitutes an exciting area for future research in this area. This endeavour could contribute to bringing genetic and cultural evolutionary approaches closer to a synthesis.

Coda – Understanding war to improve our quality of life

Intellectuals have grappled with the question of warfare for millennia and this issue remains at the top of policy makers' and international organisations' agendas – as armed conflicts throughout the world change in nature but remain, unfortunately, widespread (Johnson and Toft, 2014; Lopez, 2016; Glowacki, et al., 2017). The evolutionary human sciences – which have recently witnessed great development and flourishing – promise to help finding solutions to the issues human communities currently face. This will be achieved through an increased understanding of our own behaviour and of ways to change it to improve our quality of life (Alexander, 1979, 1987; Stearns, 2007, 2012; Michie, et al., 2017; Wells, et al., 2017; NHB Editors, 2017; Norris, et al., 2019). I hope that the studies of incentive differences to influence or perform behaviours in the context of warfare – offered in this thesis – will contribute to this effort.

Specifically, I am convinced that an evolutionary study of intergroup violence can benefit human societies in two main ways. Firstly, it can help us develop policies and strategies to prevent coalitionary aggression at multiple levels. It has been suggested that this can be realised through a greater understanding of the ecological, sociocultural, and psychological underpinnings of intergroup aggression and negative bias against outgroup members (van Vugt, 2009; McDonald, et al., 2012; Wrangham and Glowacki, 2012; Zefferman and Mathew, 2015). In this thesis, I have explored conditions under which the different parties involved in intergroup conflict might be in disagreement over actions to be taken (Ch. 2-5). In the long term, awareness of these conflicts could contribute to shaping interventions to decrease various phenomena of collective violence, from international terrorism to fights between teenage gangs (cf. efforts to develop public health response to violence; Slutkin, 2017; Slutkin, et al., 2015). Awareness of conflict and disagreement within a group could guide initiatives to limit violence, while concentrating on making the interests of different sub-groups converge towards positive outcomes (replacing competition with cooperation).

Secondly, clarifying the evolutionary-ecology of intergroup aggression can facilitate the identification of genes underlying maladaptive behavioural disorders. Recent years have seen a booming interest in making evolutionary thinking central to the medical sciences (‘evolutionary medicine’; Nesse and Stearns, 2008; Stearns, 2012; Nesse, et al., 2010;

Stearns and Medzhitov, 2015; Gluckman, et al., 2016) and thus informing public health decisions (‘evolutionary public health’; Nesse and Stearns, 2008; Wells, et al., 2017). Human behaviour has been the subject of special interest: as our understanding about its multiple interacting determinants increases, there is renewed desire to employ this knowledge to improve the human condition (Stearns, 2007). My thesis has contributed to better illuminate how intragenomic conflicts can impact on warfare-related and aggression-related behaviours. In particular, I have explored how such conflicts can lead to genomic imprinting at loci underlying these behaviours and provided expected maladaptive behavioural patterns for various classes of mutations (Ch.2). In addition, my work has highlighted that these patterns differ from those for loci controlling aggression aimed at members of the ingroup (Ch.3; cf. Crespi and Badcock, 2008; Úbeda and Gardner, 2010). These predictions should help facilitate the identification of genes underlying violence aimed in-group and out-group members.

Beyond warfare, I hope that my thesis has shown that the complexity of our biology and our social living mean that our behaviours cannot be studied in isolation. Instead, analyses must consider our ecological context and the possible interactions between the many levels of our social and biological organization. Taking such an approach in the study of various aspects of our behaviour promises to bear great fruit in future years.

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