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Review

A socio-ecological perspective on the gestural communication of great ape species, individuals, and social units

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Over the last 30 years, most research on non-human primate gestural communication has been produced by psychologists, which has shaped the questions asked and the methods used. These researchers have drawn on concepts from philosophy, linguistics, anthropology, and ethology, but despite these broad influences the field has neglected to situate gestures into the socio-ecological context in which the diverse species, individuals, and social-units exist. In this review, we present current knowledge about great ape gestural communication in terms of repertoires, meanings, and development. We fold this into a conversation about variation in other types of ape social behaviour to identify areas for future research on variation in gestural communication. Given the large variation in socio-ecological factors across species and social-units (and the individuals within these groups), we may expect to find different preferences for specific gesture types; different needs for communicating specific meanings; and different rates of encountering specific contexts. New tools, such as machine-learning based automated movement tracking, may allow us to uncover potential variation in the speed and form of gesture actions or parts of gesture actions. New multi-group multi-generational datasets provide the opportunity to apply analyses, such as Bayesian modelling, which allows us to examine these rich behavioural landscapes. Together, by expanding our questions and our methods, researchers may finally be able to study great ape gestures from the perspective of the apes themselves and explore what this gestural communication system reveals about apes' thinking and experience of their world.

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INTRODUCTION

All great apes use gestures to communicate. As discrete body movements, gestures are particularly useful in dyadic social interactions where an individual wants to communicate with their partner to achieve a particular goal. Great apes use gestures to initiate grooming, to solicit copulation, to request food, to tell others to move away or move closer, to invite play, and more (Hobaiter & Byrne 2014; Graham et al. 2018). When we consider the goals that great ape gestures achieve and the contexts that apes gesture in, it seems obvious that we would expect variation in gesture usage at the levels of individual, community, and species. However, research into gesture variation has yet to frame this discussion through a socio-ecological lens. That is, the ways gestures vary have not been fully considered in terms of the impact of social structures and environmental constraints on the individuals who deploy them.

Historically, great ape gesture research has been pre-occupied with how gestures are acquired. The two main schools of thought can be broadly summarised as “ontogenetic ritualization” and “phylogenetic ritualization” – either gesture forms are acquired through ontogeny with repeated actions becoming ritualised into gestures formed from the incomplete action onsets (Tomasello et al. 1985, 1989, 1994, 1997); or gesture forms are biologically inherited, the result of selection for these communicative signals (Byrne et al. 2017). In the former, we would expect plenty of individual variation in gesture repertoires as different actions or different sections of an action become ritualised for a particular interaction partner, and in the latter we would expect very little variation at all. Implicit in both approaches is that variation in form comes from individual experiences or genetics, but what about an individual’s role within their group and how their group is structured? Or how an individual’s environment physically limits the development and deployment of their communication strategy?

Importantly, neither approach fully grasps the ways in which gesturing can vary. As in many other systems of communication, from human language to bird song, variation in available signal types and repertoires represents only one dimension, with many others going largely unexamined. Communication may vary in terms of the overall rate of signal production as well as the rates of production for specific signal types, contexts, and meanings; the speed, size, or amplitude of whole signals or parts of signals; the types of objects that are used as part of the signal. And this variation may occur in response to diverse socio-ecological factors, from vegetation density and object availability to social relationships, reproductive status, and more. Expanding the search for variation in gesture is obviously important for questions around gesture ontogeny and gesture usage more generally, but also contributes towards wider discussions on primate culture.

In theory, any communication system should be adapted, whether through evolutionary selection or learning processes or a combination of both, to the socio-ecological niche in which it is employed (Seyfarth & Cheney 2017). Across great apes, there is substantial variation in both the physical and social environments of individuals, groups, and species. Their habitats include densely vegetated rainforests (montane and lowland), swampy woodlands, and open savannah (Caldecott & Kapos 2005). While some generalisations may be made about each species’ habitat, for example: high variability in seasonal

fruit availability for orang-utans (*Pongo* sp.; Marshall et al. 2008), there is of course variation among communities within each species. Unfortunately, some habitats are more well-studied than others. For bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) most research has taken place in rich rainforest habitats, and this has (until recently) shaped our understanding of these species (Miles & Annan 2005). However, there are bonobo communities living in savannah mosaic habitats (e.g., Manzano bonobos: Pennec et al. 2016), and the largest populations of West African chimpanzees (*Pan troglodytes verus*) occupy savannah woodland (Kalan et al. 2020). These landscapes vary dramatically with respect to how easily gestures (or other signals) can be transmitted between individuals. Incorporating the physical environments of great apes into our understanding of their communication systems is vital for revealing their full and diverse behavioural repertoires.

Within these varying physical environments, great apes also exhibit variation in their social environments. Most primate species are highly social (e.g., Shultz & Dunbar 2007; Shultz et al. 2011), and extended sociality and affordances of group-living are thought to be important driving factors of primate intelligence and cognitive complexity (Ghazanfar & Santos 2004). However, there isn't one standard "primate social grouping pattern"; in contrast, groups vary dramatically, for example in their social composition, size, and cohesiveness (Shultz et al. 2011). In great ape species grouping patterns range from the large but highly fission-fusion units of East African chimpanzees (*Pan troglodytes schweinfurthii*, e.g., Nishida 1968; Pepper et al. 1999) to the semi-solitary living orang-utans with long mother-offspring association (Singleton & van Schaik 2002; van Noordwijk et al. 2009). Within each species of great ape, social environments and experiences also vary at the level of social units and of individuals. Given the importance of gestures in dyadic communication, the ways that groups and individuals relate to one another (e.g., cohesiveness, tolerance, hierarchy, sex, age, local culture, or traditions) are likely to impact the gestural communication strategies that they deploy.

As we move beyond the focus on gestural repertoires and gesture acquisition, it is apparent that the study of wild great ape gestures must incorporate a socio-ecological perspective. In this review, we give evidence of variation in great ape communication and other social behaviour at the levels of species, individual, and social-unit, and use this evidence to guide our predictions on socio-ecological variation in great ape gesture usage.

(SUB)SPECIES VARIATION IN GESTURE USE

There seems to be a large overlap in the species-typical gestural repertoires of all great apes. When compared with chimpanzees, bonobos had a ~ 90% overlap, gorillas (*Gorilla* sp.) had a ~ 60% overlap, and orang-utans – for whom we have limited data – are estimated to have a 50–80% overlap in overall gesture repertoires (Hobaiter & Byrne 2011a; Byrne et al. 2017; Graham et al. 2017; Knox et al. 2019). As available data have increased, patterns of overlap have tended to increase (Byrne et al. 2017). All species of great apes share a common ancestor, a similar body-plan, and – to an extent – similar life history, and so the large overlap of gesture types is not particularly surprising. However, great ape species (and subspecies) experience species-typical variation in habitat type, food availability, and group size, composition, and structure. At the (sub)species level, these factors may contribute to different patterns of gesture usage, for example: preferences for certain gesture types, modalities, or the frequency of needing to request a particular goal.

Variation in habitat features, such as the density of vegetation, degree of arboreality, seasonal availability of food resources (e.g., fruit vs herbaceous vegetation), and the abundance of food resources requiring complex food processing (Byrne & Byrne 1993) can all shape aspects of primate group-living and cognition. The extent of this behavioural plasticity is also seen in atypical captive environments, for example, while it is effectively absent in wild populations, most gorillas and bonobos engage in habitual tool use in captivity (gorillas: e.g., Parker et al. 1999; bonobos: e.g., Roffman et al. 2015). Reliable inter-species differences in socio-ecology may similarly directly impact gesture usage in a number of ways.

The impact of physical environments

One feature of ape gestural repertoires is that they incorporate signals of different modalities – visual, audible, tactile, and combinations of these. Given the evidence that apes select specific modalities of gesture to match a recipient’s ability to detect them (Liebal et al. 2004; Cartmill & Byrne 2007; Hobaiter & Byrne 2011a), variation in species’ physical and social environments may bias a species use of the large gesture repertoires available towards particular forms. Species who live in visually dense habitats and/or who forage extensively on terrestrial herbaceous vegetation [e.g., mountain gorillas (*Gorilla beringei beringei*: Rothman et al. 2007) and – to some degree – bonobos (Malenky & Wrangham 1994; Furuichi et al. 2015)] may increase the use of audible and/or contact gestures in order to increase signal transmission. Greater proportions of terrestrial herbaceous vegetation foraging and more cohesive ranging (e.g., in mountain gorillas vs lowland gorillas (*Gorilla gorilla*: Doran & McNeilage 1998; Yamagiwa 1999; Yamagiwa et al. 2003) may also be accompanied by increased use of contact gestures because individuals spent more time in direct reach of each other. On the other hand, individuals living in the more open savannah and savannah-woodland habitats {some communities of chimpanzees [e.g., Fongoli chimpanzees (Senegal): Pruetz & Bertolani 2009, and Issa chimpanzees (Tanzania): Piel et al. 2017] or bonobos (e.g., Manzano bonobos: Pennec et al. 2016, and Malebo bonobos: Serckx et al. 2015)} might employ visual signals more frequently. More widespread arboreality, as in the almost consistently arboreal orang-utans (Thorpe & Crompton 2006), may be accompanied by further restrictions in limb use and/or gesture choice. For example, we would predict less frequent use of manual (and certainly bimanual) gestures as compared to more terrestrial species, given the need to use their hands for climbing and support. And indeed, while they do regularly employ their hands and arms in gesturing, they are more flexible than chimpanzees in incorporating the use of their feet and legs when producing the same gesture types (Knox et al. 2019).

Other environmental factors, such as food availability, may indirectly impact gesture usage through potential effects on group size and structure (e.g., in chimpanzees: Doran 1997; Itoh & Nishida 2007). Orang-utans have the highest seasonal variation in fruit availability of all great apes, and this may contribute to why individuals are so spatially dispersed through their range (van Schaik et al. 2009). The limited opportunities for diverse partners in proximate social interactions among orang-utans focuses their gestural communication on repeated interactions between the same individuals, typically maternal kin, and limits those with non-kin or similar age peer-groups. Orang-utans were found to be highly responsive in their gesturing, typically

responding before their partner's gestures were completed, perhaps as a result of their familiarity (Knox et al. 2019). Interestingly, in the unusual socio-ecological contexts of captivity where orang-utans are kept in atypically large social groups and experience a more terrestrial lifestyle, their repertoires of regularly used signals were larger (Fröhlich et al. 2021). The majority of these apparently novel "inventions" were gesture types typical in other ape species (e.g., cf. Fröhlich et al. 2021 with Byrne et al. 2017), suggesting that while immediate socio-ecology shapes local repertoires in particular ways, apes retain access to shared ape-typical sets of available signals.

In some habitats, apes have developed complex feeding techniques to access valued food resources. The presence of cognitively complex problem-solving in one domain (e.g., foraging) may promote greater flexibility in other cognitively challenging behaviours such as (gestural) communication (Kolodny & Edelman 2018). (Sub)species showing variable repertoires of hierarchically structured actions, for example in tool-assisted extractive foraging [chimpanzees and orang-utans (van Schaik et al. 2003; Sanz & Morgan 2010; Hayashi & Inoue-Nakamura 2011)] or in other elaborate food processing techniques [e.g., mountain gorilla thistle and nettle foraging (Byrne & Byrne 1993)] may also be more diverse in the structuring of their gestural signals and combinations than those that do not.

The impact of social environments

Across species, both the overall organisation and the composition of social units can be (largely) consistent (chimpanzees and bonobos: hierarchical multi-male/multi-female associations; Gruber & Clay 2016) or highly variable (gorillas: one-male/multi-female, multi-male/multi-female, and occasionally all-male units, with (sub)species differences; Yamagiwa et al. 2003; Robbins & Robbins 2018). Variation in social unit organisation may result in varying gestural patterns between units. Thus, gestural variation across social units may be more pronounced in gorillas, as compared to the more uniform social systems of chimpanzees and bonobos.

As a consequence of the different social roles and relationships of females and males across great ape (sub)species, we are likely to observe some sex differences in gestural behaviour. Males are dominant in gorillas (Robbins & Robbins 2018) and chimpanzees (Gruber & Clay 2016), while females tend to be dominant over or at least co-dominant with males in bonobos (Parish 1996; Paoli et al. 2006; but see White & Wood 2007). There are also underlying species differences in hierarchies, which may be steep and nonlinear with one dominant individual having no or few within-group competitors [silverbacks in most gorillas, although male within-group competition is present in multi-male/multi-female mountain gorilla groups (Sicotte 1994; Stoinski et al. 2009)], or more linear with one dominant individual and other competing ranks present [e.g., chimpanzees: most prominently seen in males (Gruber & Clay 2016); although a hierarchy among females is also usually present, if flatter (Pusey & Schroepfer-Walker 2013)]. In some species it remains unclear if hierarchies are absent, or just harder to detect (female mountain gorillas: Robbins & Robbins 2018). Further variation between species is found in the stability of these hierarchies. A particular hierarchical structure may be quite stable over time (e.g., in mountain gorillas, silverback tenures last on average 12–15 years; Robbins et al. 2019; and in female chimpanzees, individuals typically form fairly stable queues for rank; Foerster

et al. 2016) or dynamic with turnovers happening more frequently (e.g., in male chimpanzees; Foerster et al. 2016).

Species differences in social bonds likely also shape species differences in gestural communication networks: who communicates with whom and about what. Depending on species, social bonds may be mediated through cooperative behaviours, such as hunting, food sharing (e.g., chimpanzees: Wittig et al. 2014; Samuni et al. 2018a, 2018b and bonobos: Fruth & Hohmann et al. 2002; Goldstone et al. 2016), and border patrols (West African chimpanzees, Samuni et al. 2019), or other forms of social interactions such as grooming and socio-sexual behaviour (chimpanzees: e.g., Crockford et al. 2013; Sandel & Reddy 2021; bonobos: e.g., Moscovice et al. 2019; gorillas: Yamagiwa 1992; Robbins 2010; Grueter & Stoinski 2016). Chimpanzees tend to have strong male-male social bonds and weaker female-female social bonds; however, female social bond strength is variable across subspecies with a tendency for weaker bonds in East African compared to West African chimpanzees (Yamakoshi 2004; Lehmann & Boesch 2008). In contrast, bonobos usually have weaker male-male social bonds and strong female-female social bonds (Tokuyama & Furuichi 2016). In gorillas, male-male behaviour is dependent on social unit composition – males in all-male units are generally more aggressive towards each other but also frequently engage in affiliative and socio-sexual interactions, which are less commonly observed in mixed-sex gorilla units (Yamagiwa 1992; Robbins 2010). Gorillas tend to have very weak female social bonds (Grueter et al. 2016), however, affiliative and socio-sexual interactions can be relatively common in some (sub)species (Grueter & Stoinski 2016). Across great ape species, male-female association may be strong [e.g., in bonobos [Surbeck et al. 2017a; especially between mothers and sons (Surbeck et al. 2011)] and in gorillas (strongest bonds in a given unit; Harcourt & Stewart 2007)] or apparently variable depending on (sub)species (e.g., West as compared to East African chimpanzees, Lehmann & Boesch 2008). Species differences in social bonds and association may be reflected in their communication networks, although little research has so far examined the impact of these social structures on gestural communication (but see: Roberts & Roberts 2016).

Group cohesiveness also varies across great ape species. While chimpanzee and bonobo social units are usually larger than gorilla units or the temporary social fusions of adult orang-utans, chimpanzees and, to a lesser extent, bonobos employ fission-fusion social organisation that means that the whole unit group rarely – if ever – ranges together at the same time (Nishida 1968; Kano 1982; White 1988). In contrast, gorillas generally form more stable social units (Robbins & Robbins 2018; however, lowland gorillas occasionally divide into subgroups (Tutin 1996; Remis 1997; Yamagiwa et al. 2003). Where social units fission into smaller fluctuating subgroups during the day, the opportunity for gestural interaction is temporarily limited to individuals present in the current subgroup and any communication directed at other social unit members will usually involve long-distance signals. While chimpanzees, bonobos, and gorillas all have long-(buttress drumming) or medium-distance (chest-beating) gesture forms, they are rarely classed as fully intentional gestures due to the difficulties in identifying the communicative partner. Size and social composition (in terms of age and sex ratio) of great ape subgroups may vary dramatically [for example: with seasonality (Doran 1997; White 1998; Wich et al. 2006)] and with it the gestural interactions likely to be observed at a given time. Fissions may be frequent with

subgroups tending to be smaller and skewed in terms of age and sex [most often observed in East African chimpanzees (Nishida 1968)], or less frequent with resulting subgroups larger [e.g., in bonobos (Kano 1982)] and/or more mixed [some populations of West African chimpanzees (e.g., Tai: Lehmann & Boesch 2005; and bonobos: Kano 1982)].

In contrast, in gorillas' cohesively ranging social units (Doran & McNeillage 1998), group composition, and with it the range of possible interaction partners, remains relatively constant. As a result, the gestural behaviour of any one individual may reflect that of the overall social unit structure more directly (especially in the very cohesive mountain gorillas). With group members in more constant proximity, individuals may be generally more tolerant of the close presence of others and perhaps more inclined to use contact gestures. Indeed, given that female gorillas can emigrate to multiple groups – leaving their independent children behind if parous (Robbins & Robbins 2015) – gorilla gestural behaviour may be more coherent across local social units. Similarly, bonobo communities engage in extended periods of social interaction across neighbouring social units – ranging together and sharing food and other affiliative behaviour for hours or even days (Sakamaki et al. 2018), contexts that are likely to include extensive gestural exchanges (Graham et al. 2017).

Throughout much of this section, orang-utans have been conspicuous by their absence. Of all the non-human great apes, we know the least about their gestural communication outside of captivity, and their largely solitary lifestyles mean that opportunities for gestural communication are limited largely to mother-infant dyads (Fröhlich et al. 2019; Knox et al. 2019). Females in one territory are often related and may forage together occasionally while staying in ranging proximity of a dominant resident male. Direct adult male-female interactions are often limited to the sexual context, although subadult individuals may occasionally encounter each other and range together. Opportunities for observation of gestural communication are further compounded by their highly arboreal lifestyle and, with limited data, disentangling species, social unit, and individual difference is likely to be particularly challenging.

INDIVIDUAL VARIATION IN GESTURE USE

Socio-ecological factors likely impact how different great ape species deploy gestures and, at the other end of the spectrum, they are also likely to affect how “individual” apes deploy gestures. Research that considers individual variation in gestural communication has been largely concerned with variation at the level of gestural repertoires. However, gesture usage can vary in numerous other ways, including (but not limited to) the rates at which individuals deploy certain gesture types and modalities for certain meanings, preference for certain body parts, gesture laterality, and use of certain objects alongside gestures. An individual's place within their social environment may affect how they deploy gestures. For example: personal network size, experience, ontogeny, age, rank, and sex have all been found to affect gesture use (e.g., Roberts & Roberts 2016; Fröhlich et al. 2017). The diversity and frequency of social interactions with other individuals impacts different individuals' experiences of gesture use. Similarly, the role an individual plays within the community, for example: their position within the hierarchy, could result in biases towards using particular

types or modalities of gesture. Here, we focus on three aspects of individual identity: how ontogeny and age, sex, and rank affect gesture use in great apes.

Ontogeny and age

The onset of gesture production in great apes has been studied most extensively in chimpanzees, with both captive and wild studies indicating that the social environment plays a crucial role in the development of an individuals' communicative abilities. The absence of particular figures – such as early maternal loss – or of other typical social interactions during ontogeny, has a profound impact on social behaviour in adulthood (van Leeuwen et al. 2014; Stanton et al. 2020). In both wild and captive settings, conspecific interaction represents a significant driver of gestural development (Tomasello et al. 1989, 1994, 1997; Hobaiter & Byrne 2011a, 2011b; Schneider et al. 2012a, 2012b; Bard et al. 2014; Fröhlich et al. 2016a, 2016b, 2017).

By selecting with whom they interact, chimpanzee mothers influence their offspring's social environment (Murray et al. 2014). Infants of more gregarious mothers are exposed to a greater number of conspecific interactions during which they can test their signalling abilities, giving them an early advantage in entering the community's social world. For example, in a longitudinal captive study on gesture development, the chimpanzee who was the least independent from their mother (i.e., was in close contact most of the time), was also the individual with the latest gestural onset among conspecifics (Schneider et al. 2012b). Similarly, individual repertoire size and frequency of gesture use in chimpanzee infants are strongly associated with the number of conspecific interaction partners (excluding mothers) in the previous month of life (Fröhlich et al. 2017). The effect of sociality on infant gestural development is also likely in other great ape species. Orang-utans become independent from their mothers later than other species of great ape, and the onset of gesture production for orang-utan infants appears to be several months later than other ape species (Schneider et al. 2012a), with intentional communication emerging between 2.5 and 5.5 years of age (Bard 1987).

Once individuals have started producing gestures, their degree of use of the gestural repertoire tends to increase with age for all ape species, before declining again in adulthood. In gorillas, the number of gesture types used increases until about 3–4 years of age, followed by a decline (Pika et al. 2003). Similarly in chimpanzees and orang-utans, the number of gesture types used increases across infancy, peaking in juveniles, before declining in maturity (5–10 years old; Tomasello et al. 1985, 1997; Pika et al. 2003; Liebal et al. 2006; Cartmill 2008; Hobaiter & Byrne 2011a). Species' differences in gesture development may be related to species' differences in overall development. Among African apes, gorillas have shorter infant and juvenile stages (Pika et al. 2003) and develop aspects of physical maturity and intellectual capacity at a younger age than chimpanzees (Spinozzi & Natale 1989; Parker et al. 1999).

Orang-utans showed little variability in the types of gestures used within age classes, with mother-infant dyads using the same travel-initiation gestures as other members of their age group (but different from other age groups; Cartmill & Byrne 2010), while chimpanzee mothers living in the same community used different sets of gestures to initiate travel with their infants (Fröhlich et al. 2016b). However, here orang-utan data were limited to small numbers of captive individuals, and in other

settings captivity appeared to increase diversity of gesture use in orang-utans (Fröhlich et al. 2021).

Apes' use of different gestural modalities also varies with age, with most individuals employing tactile gesture types before or at a similar time to visual ones, with audible gesture types being used later in development (Schneider et al. 2012a). Shifts with age in the use of particular gesture types or modalities may result from changes in the goals and contexts that gestures are used for (for example: a decrease in play, or an increase in behaviour such as sexual solicitation or agonistic interactions), reflecting different selection from within the available repertoire (Hobaiter & Byrne 2011b; Knox et al. 2019). Captive bonobos, who typically engage in substantial amounts of play even in adulthood, deployed a large stable repertoire in maturity (Demuru et al. 2015), perhaps due to the continued use of play-related gesture types less used by chimpanzees during adulthood.

Laterality of gesture movements has also been found to change with age. In gorillas, right-handedness increased with signaller's age up until adulthood, followed by a decrease in later life (Hopkins & Leavens 1998; Prieur et al. 2016). Given that laterality also appears to be impacted by arousal (Prieur et al. 2016, 2017), the increase and later decrease of laterality with increasing age might result from variation in the behavioural contexts in which gorillas used their gestures in their adult peak, as compared to earlier or later in life (Prieur et al. 2016). How laterality changes within a chimpanzee lifetime remains unclear: older captive chimpanzees were observed to perform more right-hand gestures (Hopkins & Leavens 1998), while in wild chimpanzees the use of gesture forms that include an object appeared to increase right-handedness (Hobaiter & Byrne 2013).

Sex

Great apes show sex differences in their gestural communication, likely a reflection of sex differences in social behaviour rather than in the communicative system itself. For example: infant male chimpanzees gestured more frequently and employed a larger range of gesture types (Fröhlich et al. 2017). Early socialisation plays a crucial role in the development of male chimpanzees, particularly given the importance of social dominance and reproductive strategies in adulthood (Muller & Mitani 2005), where strong male-male social bonds can lead to increased reproductive success and dominance rank (Gilby et al. 2013). As a result of their mothers' social behaviour, infant males tend to interact more with adult conspecifics than female infants, and in particular with adult males (Lonsdorf et al. 2014a, 2014b), increasing their exposure to a wider range of gestures and gesturers. The increased frequency and diversity of social interactions experienced by male infants, as compared to female infants, may underpin the greater variety of gestures that they use at an early age.

These developmental and gestural sex-differences are likely also present in other ape species, given their societal sex differences. In bonobos, individuals of both sexes expressed and understood all gesture types observed, with just one (rare) gesture type never performed towards males (Graham et al. 2017). Male and female infant gorillas differ in the types of gestures they typically employ, but both use around the same number of gesture types (Genty et al. 2009). In gorilla infants, both males and females prefer other males as a playmate. Doing so may offer males the ability to explore

agonistic behaviour through wrestle and chasing play, and females the opportunity to explore the mixed-sex social bonds important in adulthood (Maestripieri & Ross 2003).

Rank

Social communications are key to an individual's ability to develop and maintain social relationships with other group members. For example, chimpanzee pant-grunting has been suggested to reflect a caller's interaction intent, exploring receiver's motivation and mood, conveying respect (Laporte & Zuberbühler 2010), as well as a tool to avoid aggression (Fedurek et al. 2019, 2021). An individual's absolute and relative social rank has been shown to extensively impact great ape vocal communication. For example, chimpanzee pant-grunt vocalizations are almost exclusively produced by lower-ranking individuals, towards higher-ranking ones (Laporte & Zuberbühler 2010; Fedurek et al. 2019), and higher-ranking males produce more pant-hoots than low ranking individuals (Mitani & Nishida 1993) and more vocalizations than other age-sex classes in general (Clark 1993). Higher ranking gorillas give more double-calls than lower ranking individuals (Harcourt & Stewart 1996), and in bonobos, low ranking females are more likely to produce copulation calls when interacting with higher ranking females during genito-genital rubbing (Clay & Zuberbühler 2012). Given the abundance of evidence in vocal communication, and the effect of individual rank on great ape fitness (e.g., reproductive success: Cowlshaw & Dunbar 1991; Surbeck et al. 2017b; Wright et al. 2020; foraging strategies: Murray et al. 2006, 2007; innovation: Reader & Laland 2001) and vocal communication, we expect that rank also affects great ape gesture use; however, to date, there has been very little investigation of its impact on gesture.

The rank-related gestures used by subordinate individuals in interactions with more dominant individuals (e.g., "wrist present" and "rump presenting") emerged later in life in a group of captive chimpanzees, as compared to other gesture types (Bard et al. 2014). In a wild community of East African chimpanzees, male rank was found to have relatively little effect on the rate of use of gestures, with the exception of the alpha male – who was highly prolific (Hobaiter et al. 2017). Importantly, no study has yet explored the effect of rank on individual gesture use longitudinally, and the effect of rank as distinct from that of individual identity or contexts of use is yet to be properly disentangled. A more complete analysis of the impacts of rank on great ape gestural communication will require significant datasets that include multiple communities for each species and multiple individuals occupying similarly ranked positions, and – ideally – individuals varying in rank across their lifetime. In doing so these we can consider more fully how great ape individuals' communication is affected by the social structures in which they live.

SOCIAL UNIT VARIATION IN GESTURE USE

While an increasing body of research on ape gestural communication has focused on the level of either species or individual usage (e.g., Fröhlich et al. 2016a, 2017; Graham et al. 2018, 2020; Taglialatela et al. 2018; Kersken et al. 2019), there is also substantial potential for important variation in gestures between social units. As

outlined in the first section, within any single (sub)species, great ape social units can occupy dramatically different environments. Some of these differences arise from ecological variation across habitats while others arise through diverging social experiences, including cultures and traditions (Whiten et al. 1999) that may, in turn, also be shaped by the groups' socio-ecology (Koops et al. 2013, 2014). These cultural and ecological differences may influence the use of gesture, increasing variation in gesture use between – as compared to within – social units, for example: in the prevalence of particular goals or in the choice of certain gesture types to achieve a given goal.

We have already described ways in which ecological variability – such as differences in food availability and distribution – can influence the way in which individuals use gestures. Different gesture types may be produced or perceived differently in different environments, impacting their transmission efficacy. Habitat ecology can also shape social structure (e.g., Roth et al. 2020) leading to different socio-communicative strategies between, and sometimes within, species (e.g., Tagliatela et al. 2018). For example, chimpanzees use more multi-modal communication when compared to bonobos, which was suggested to result from differences in ecology and social structure between the species (Tagliatela et al. 2018). Once we have accounted for adaptations to local ecology and the impact of social environment on individual learning, remaining behavioural differences are often attributed to cultural variation or local traditions acquired through social learning (e.g., Whiten et al. 1999; van Schaik et al. 2003; Robbins et al. 2016).

Local traditions have been reported across a range of great ape behavioural contexts including tool use (Whiten et al. 1999; Boesch et al. 2020), food processing (Byrne et al. 2011; Schuppli et al. 2016), hunting strategies and prey choice (Samuni et al. 2020), social customs (McGrew & Tutin 1978), and communication (Crockford et al. 2004; Wich et al. 2012). Different social environments may promote social learning to varying degrees. For example – communities that are more cohesive provide more opportunities to interact with a wide range of individuals, potentially increasing social learning opportunities and promoting rapid transmission of novel behaviour between individuals (Muthukrishna et al. 2016). Tracking this transmission process in wild apes is very difficult, with only a handful of studies reporting the social transmission of potentially novel behaviour throughout one social unit (e.g., Biro et al. 2003; Hobaiter et al. 2014). More commonly, studies have used the “method of exclusion” – comparing the presence of a behaviour across different social units, while controlling for socio-ecological and genetic variation that could influence the presence of that behaviour within a group (e.g., McGrew & Tutin 1978; Whiten et al. 1999; van Schaik et al. 2003; Robbins et al. 2016).

The development of gestural communication, whether acquired through “ontogenetic ritualization” or “phylogenetic ritualization” (Plooij 1978; Tomasello et al. 1985, 1994; Hobaiter & Byrne 2011a; Byrne et al. 2017; Pika & Fröhlich 2019), requires repeated social interactions with other individuals. These repeated social interactions are necessary for individuals to gain a shared understanding of how to use their gestures, whether that might be a gesture's meaning or subtler nuances of context or timing. If any aspect of gesturing relies on social learning, as individuals interact more often (or even exclusively) with others from their own social unit, inter-group variation would be expected to arise over time, as rare innovations or modifications to gestural expression spread within the groups in which they emerge.

So far, studies of great ape communication have found limited evidence for cultural or inter-group variation in the gestural repertoires of gorillas (Pika et al. 2003; Genty et al. 2009), and chimpanzees (Tomasello et al. 1994; Hobaiter & Byrne 2011a). However, these studies were somewhat limited in their power to detect variation, as they often focused on time-limited snapshots of small samples. Moreover, they were restricted to comparing the presence or absence of gesture types in group repertoires and did not examine other potential sources of gestural variation. Beyond primate research, other successful studies of cultural variation in non-human communication include group-specific expression of a shared set of signals, for example through recombination in bird and whale vocalisations (e.g., Baker & Cunningham 1985; Rendell & Whitehead 2003; Fitch 2009; Garland et al. 2017).

Cultural variation has also been observed in human gestural communication. Many human gesture types (e.g., pointing, palm-up, and size gestures) are observed across a wide range of societies and have been termed “gesture universals” (Kendon 2002; Cooperrider et al. 2018a, 2018b; Cooperrider 2020). However, the way these gestures are used can vary across societies in terms of the meaning of specific gesture forms, or the frequency with which they are used for a given meaning (Jakobson 1972; Kendon 2002; Cooperrider et al. 2018b). Furthermore, some gestures may be performed with slight variation in their physical form (e.g., Enfield et al. 2007), although these may be difficult to detect in non-human apes. Finally, different groups of people use gestures at different rates when communicating (Pika et al. 2006; So 2010). For example, monolingual English speakers tend to use fewer gestures when speaking compared to bilingual English-French and English-Spanish speakers (Pika et al. 2006). Diversifying the way in which we explore potential sources of variation, will be important in our thinking about variation in non-human species as well.

Studies describing differences in cultural traits between groups already hint at some differences in gestural repertoires (Robbins et al. 2016) or the presence of actions that may be gestural but were not described as such (Whiten et al. 1999; Hohmann & Fruth 2003; van Schaik et al. 2003). Long-term systematic studies across a range of behavioural contexts may reveal more variation in gestural repertoires between great ape groups. However, the extensive overlap in great ape gestural repertoires across species (Byrne et al. 2017; Graham et al. 2017, 2018; Kersken et al. 2019) also suggests that social units are unlikely to differ in the overall repertoires of gestures available for use by an individual of that species.

In chimpanzees, anecdotal evidence suggests that the leaf-clipping gesture – used across all studied communities – may be used preferentially in different contexts between communities (Nishida 1980; Boesch 1995). Furthermore, the gesture “leaf-drop” has been reported in several bonobo communities (Kano 1997; Graham et al. 2017) and anecdotally reported in some chimpanzee communities (C. Hobaiter pers. comm.) suggesting that it may show species overlap in at least some groups. Varying levels of habituation and the lack of systematic observation across behavioural contexts means that, for now, the jury on cultural variation in gesture is still out. Nonetheless, preliminary evidence and the wider evidence for cultural variation in material culture across great ape social units (e.g., Whiten et al. 1999; Koops et al. 2014) suggests that object-use in gestural communication may be a fruitful avenue for exploring cultural variation in gestural communication in great apes. Like humans, other apes may also share a broadly universal gestural repertoire but vary in their frequency of gesture use, in nuanced forms of specific gesture types (for example: leaf-

dropping vs leaf-clipping, or leaf-clipping with the hands or with the mouth), and in preferences for certain gesture forms in different contexts or to convey particular meanings.

Indeed, it may be mal-adaptive for great ape gesture use to vary dramatically in fundamental characteristics of the available repertoire across groups, as most ape species exhibit some degree of transfer between social units, with either one or both sexes dispersing from their natal community at some point in their lives (Robbins et al. 2009; Morrogh-Bernard et al. 2010; Nietlisbach et al. 2012; Ishizuka et al. 2019; Walker & Pusey 2020), and bonobos engaging in positive encounters that involve communication among members of neighbouring units (Idani 1990). These patterns of dispersal and socialisation may hinder the emergence of large-scale differences in gestural repertoires. Other forms of variation may still be present, allowing individuals to communicate in more similar ways to individuals within their immediate social unit while retaining the flexibility to communicate with individuals from other groups.

DISCUSSION

You will have likely noticed when reading how much of this “review” is speculative and involved reasoning across from other areas of great ape behaviour. While great ape gestures were included in Darwin’s writings in 1872, their in-depth exploration as a field of study spans just a couple of decades. Much of this research has come from a cognitive perspective – doing the important work of establishing that this system of communication is flexible and involves the intentional sharing of goals between specific communicative partners (Tomasello et al. 1985, 1989; Pika et al. 2003; Liebal et al. 2006; Cartmill & Byrne 2007, 2010; Hobaiter & Byrne 2011a, 2011b, 2013, 2014; Bard et al. 2014; Roberts et al. 2014; Byrne et al. 2017; Fröhlich et al. 2017; Graham et al. 2018, 2020). To do so, researchers initially focused their efforts on small captive groups of apes in which clear reliable observations could be made (chimpanzees, *Pan troglodytes*: Tomasello et al. 1985, 1989; gorillas, *Gorilla gorilla*: Tanner & Byrne 1996; Pika et al. 2003; bonobos, *Pan paniscus*: Pika et al. 2005; Halina et al. 2013; orangutans, *Pongo abelii/pygmaeus*: Liebal et al. 2006; Cartmill & Byrne 2007); it is only over the past 10-years that the field of ape gestural research has gone back to the wild: studying ape gesture in situ. Doing so was fundamental – rather than a system of communication predominantly used by young apes in play (Tomasello et al. 1985, 1989; Tanner & Byrne 1996; Pika et al. 2003), we recognised the central importance of gesture to every aspect of ape lives (Hobaiter & Byrne 2011a, 2011b, 2014; Byrne et al. 2017; Graham et al. 2017). That, in turn, means that it has become increasingly important to understand the socio-ecological context in which apes employ their gestures. Systems of communication, like other behaviour, are adapted to the niche in which they are used (Seyfarth & Cheney 2017), as a field, we are only starting to ask the questions of how an ape’s physical and social environment impacts her gesturing.

Research into species, individual, and group differences in gestural communication is currently lagging behind the vast range of projects studying variation in other areas of great ape behaviour. Lack of data, inadequate sampling techniques, and our physical and statistical limitation in quantifying nuanced variation in gestural communication likely all contribute to this lag. With more habituated groups, advances in

video recording, data storage, video tracking technologies, we may now be ready to take a deeper look into great ape gestures than ever before. Doing so properly will take truly vast quantities of data – to address the types of topics we have outlined throughout this review, we need datasets that are typically larger than any one individual researcher’s ability to accumulate. Collaboration and open-science practices will be key to taking the study of gesture to greater depths of questioning. It is more than simply accumulating more pieces of the puzzle – there are some questions you can only address at scale when you put the pieces together.

Today, we recognise the importance of sampling diversity in our studies of human behaviour (Henrich et al. 2010), particularly where we want to be able to describe species-typical traits, and/or the range of behaviour present. With large datasets of ape gesture, in which we sample across individuals, groups, generations, populations, and (sub)species, we incorporate vital diversity into our great ape data (Leavens et al. 2010; Voelkl et al. 2020; Webster & Rutz 2020). Another significant advance will be in the tools that we have available to us. With new video coding software, for example: DeepLabCut (Mathis 2018) or SLEAP (Pereira et al. 2020), we can track the precise movement paths associated with specific gesture instances and identify common features within a gesture “type” or more objectively compare them across individuals and groups. Historically, we were only able to quantify and statistically compare characteristics of vocalisations with the advent of programmes that allowed us to measure pitch and frequency (e.g., Crockford et al. 2004). Now, researchers are able to use deep machine learning to recognise primate faces and identify individuals (Witham 2018; Schofield et al. 2019), and use markerless motion tracking software to identify poses, movement, and even certain behaviour (Labuguen et al. 2019, 2020; Bala et al. 2020). These recent advances mean that we can start to do the same with gestures. Similarly, recent decades have seen substantial advances in our statistical tools from dynamic Social Network Analyses that allow us to more directly trace the transmission of behaviour (Hobaiter et al. 2014) to the Generalized Linear Mixed Models and Bayesian approaches that allow more sophisticated analysis of the large, rich, messy, datasets that reflect real-world behaviour (for example: Bolker et al. 2009; McElreath 2018).

Now that we are starting to accumulate those datasets and tools, what should we do with them? A theme throughout this review is the diversity of experience a single ape of any species might be exposed to. In addition to important species differences, ape behaviour is highly flexible, and the range of group and individual variation expressed within a species is impressive. We recognise that diversity in our datasets is key to avoiding bias in our descriptions of group and species behaviour – but it is more than that. Variation is, in itself, an opportunity to ask interesting questions. Given apes’ long lives, varied social relationships, and meaningful cognitive similarities to humans, we can also ask interesting questions from a socio-ecological perspective, in particular about the level between species genetics and individual experience: the social unit. Our studies of non-human ape culture have typically focused on differences in materials and objects, in many cases: tool use (Boesch & Boesch 1983; Brewer & McGrew 1990; Whiten et al. 1999, but cf. Boesch et al. 2020). Our studies of human culture encompass much more: from dialect and song, to gendered group norms about dress, or cultural norms about milk in tea and ice in whisky. To what extent is an individual ape independent of her genetic endowment or individual experience? Do stable differences in ape socio-ecology, given our understanding of

other apes' shared capacity for recognising others' behaviour and mind (Hare et al. 2001; Krupenye et al. 2016; Crockford et al. 2017), lead to established differences in social "norms"? If so, gesture may be particularly well suited to exploring them – the very large repertoires of signals, with scope for flexibility and individual expression, offers a potential to be a tool with which we can explore other aspects of ape cognition that are not directly observable. When an ape gestures, she has something "in mind"; understanding ape gesture from the perspective of the ape who is using it, allows us to ask questions about how their genetics, socio-ecology, individual differences, and group-cultures impact their thinking and experience of their world.

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AUTHOR CONTRIBUTION

Authors contributed equally to this paper. Middle authorship order was decided randomly, by two guinea pigs picking cucumber pieces with the authors' initials on them out of a pot.

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