Avian distraction displays: a review

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Distraction displays are conspicuous behaviours functioning to distract a predator's attention away from the displayer's nest or young, thereby reducing the chance of offspring being discovered and predated. Distraction is one of the riskier parental care tactics, as its success derives from the displaying parent becoming the focus of a predator's attention. Such displays are prominent in birds, primarily shorebirds, but the last comprehensive review of distraction was in 1984. Our review aims to provide an updated synthesis of what is known about distraction displays in birds, and to open up new areas of study by highlighting some of the key avenues to explore and the broadened ecological perspectives that could be adopted in future research. We begin by drawing attention to the flexibility of form that distraction displays can take and providing an overview of the different avian taxa known to use anti-predator distraction displays, also examining species-specific sex differences in use. We then explore the adaptive value and evolution of distraction displays, before considering the variation seen in the timing of their use over a reproductive cycle. An evaluation of the efficacy of distraction compared with alternative anti-predator tactics is then conducted via a cost-benefit analysis. Distraction displays are also found in a handful of non-avian taxa, and we briefly consider these unusual cases. We conclude by postulating why distraction is primarily an avian behaviour and set out our suggestions for future research into the evolution and ecology of avian distraction displays.

Keywords: Anti-predator defence, Behavioural ecology, Evolution, Nest defence, Parental care, Predator distraction

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Avoiding and escaping from predators is an essential part of life for animals, and prey species have evolved a wide range of defensive adaptations for that purpose. As an individual's fitness is dependent on passing on its genetic material successfully to descendants beyond the subsequent generation, there are many cases where prey individuals not only defend themselves but also defend their offspring. Parents of various taxa respond to approaching egg- or brood-predators using a range of 'nest protection' behaviours (Murphy 1926). Although these behaviours can take several different forms, the options involved are often not mutually exclusive and can be used flexibly depending on context. Nest protection can comprise cryptic behaviour (Endler 1978, Baker & Parker 1979, Gochfeld 1979, Kreisinger & Albrecht 2008, Caro 2014), aggression (Larsen 1991, Burger & Gochfeld 1992, Larsen *et al.* 1996, Ylieff *et al.* 1998, Carrillo & Aparicio 2001, Campobello & Sealy 2010, Jónsson & Gunnarsson 2010, Sherbrooke 2017), defensive defecation (McDougall & Milne 1978, Meilvang *et al.* 1997), and so-called 'distraction displays' (Williamson 1949, 1952, Nice 1964, Gochfeld 1984). Of these we focus on distraction displays, an anti-predator defence that arguably encompasses some of the most eye-catching parenting behaviours found in the animal kingdom.

Knowledge of distraction displays – the most well-known type being 'injury-feigning' behaviour – dates back to at least Aristotle (Davis Jr. 1989). However, many older scientific reports of this behaviour have been primarily descriptive (Gochfeld 1984) and a new review of the subject consolidating these works with more recent, quantitative efforts is long overdue. The behaviour has been variously referred to as diversionary behaviour with multiple sub-categories (Armstrong 1949a, b, Hebard 1950, Gramza 1967), waving display (Clemmons & Lambrechts 1992), 'paratreptic' behaviour that leads a predator away from a nest (Smith 2017), and conspicuous behaviour (Giroux *et al.*, 2016), but we prefer the most commonly-used term ‘distraction displays’ (Williamson 1949, 1952, Nice 1964, Gochfeld 1984, Caro 2005). We start by providing what we intend to be a unifying definition of distraction. Unifying the concept in such a way will allow researchers to integrate and compare findings more easily, generating a richer overall understanding of what is a conspicuously variable defence.

We define distraction displays as:

“***behaviours functioning primarily to increase the conspicuousness and/or apparent attractiveness of the displayer to a predators, and thus distract a predator’s attention away from a nest or young and towards the displayer, thereby reducing the chance of offspring being discovered and predated***”.

Distraction is unusual as an anti-predator defence in that it does not function to hide the prey or advertise it as an unattractive quarry; conversely, it often makes the displaying prey appear more appealing. A salient characteristic of distraction, therefore, is that the predator does not simply break off its search but instead switches its focus to the displayer. In this way, distraction displays are conceptually distinct from intimidation of predators, or signalling of perceptual awareness (where the prey signals to the predator that it has been detected). Important to our definition is that the behaviour must function *primarily* to distract. We acknowledge that some behaviours serve multiple functions and that their secondary functions may fall under the rest of the definition, but for a behaviour to be classed as distraction we consider that its main function should be to distract. For example, alarm calling is certainly a conspicuous behaviour that may well attract a predator’s attention towards the caller. However, its primary function is generally considered either to alert conspecifics of a threat or to signal to a predator that it has been detected. If these were secondary to the attraction of the predator's attention to the displayer and away from young, then the calling would be considered a distraction display.

The last comprehensive review on the topic of distraction displays is Gochfeld's (1984) chapter 'Anti-predator behavior: Aggressive and distraction displays of shorebirds'. As suggested by the title, this work has a specific taxonomic focus. Indeed birds, and especially shorebirds (Charadriiformes), are the taxa most commonly reported to use distraction behaviour to defend their young. However, while most of the literature still concerns shorebirds, distraction displays have since been reported in a wider variety of avian taxa and research has advanced understanding of the behaviour in the last few decades. In this review, we aim to provide an updated synthesis of what is known about distraction displays in birds and encourage further studies into this fascinating anti-predator defence. We begin by discussing the forms distraction displays can take, the wide but sparse occurrence of the defence in avian taxa, and the variation found in characteristic sex roles (an important consideration given the differential parental investment often reported in birds). The ecology and adaptive value of distraction displays are then considered, followed by discussion of the timing of distraction display use during reproduction. A large section of the review is then dedicated to a cost-benefit analysis of the behaviour, evaluating the efficacy of distraction compared with alternative anti-predator tactics and considering the many trade-offs involved. We then outline the apparent use of distraction displays in a handful of non-avian taxa, highlighting why non-avian instances of distraction display defence are so rare. Finally, we outline what we believe to be the most interesting avenues for future research into the evolution and behavioural ecology of avian distraction displays.

Form and occurrence across avian taxa

Distraction displays encompass some of the most flamboyant and eye-catching parental care behaviours seen across any taxa in the natural world. Injury-feigning is by far the most commonly-described form and the archetypal example, often used synonymously, is the 'broken-wing' display in which the (uninjured) parent bird moves across the ground apparently feigning an inability to take flight (Barash 1975, Wiklund & Stigh 1983, Gochfeld 1984, Burger *et al.* 1989, Byrkjedal 1989, Davis Jr. 1989, Kameda 1994, Wijesinghe & Dayawansa 1998, Leite *et al.* 2012, Wang *et al.* 2013, Caro 2014, Gómez-Serrano 2018). However, distraction displays can take a great many forms in birds, ranging from relatively simple movements while standing still, to eye-catching flying and running activities. Displacement-type displays constitute a further variant, where an adult prey individual leaves its nest and engages in behaviour that seems unrelated to defending their nest or young (Gochfeld 1984). Table 1 outlines some of the main categories and sub-categories that have been used to classify distraction displays (Gochfeld 1984, Caro 2005, Gómez-Serrano 2018), alongside some examples of bird species using these behaviours. Further variations on distraction also exist in the literature, and "coordinated misdirection" is a recently identified example, wherein birds flying as a pair co-operate such that one parent returns to the nest while the other veers away to draw the attention of nest predators (Gulson-Castillo *et al.* 2018).

From Table 1, it is evident that distraction is a widespread but patchily distributed defence amongst birds. Nice (1964) cited thirteen orders and sixteen passerine families that use distraction displays to defend their young (Davis Jr. 1989) and Gochfeld (1984) documented their prevalence in shorebirds in particular. Shorebirds are considered to face a trade-off in selecting nest sites (Götmark *et al.* 1995, Gómez-Serrano & López-López 2014), choosing primarily between a cryptic strategy – nesting in habitats with dense and tall vegetation as a means by which to camouflage clutches against predation – and a predator detection strategy, where parents nest in open habitats to increase visibility and the early detection of threats. Which option birds choose may depend on the predator community present and the risk of predation at each stage of reproduction, but certainly many shorebirds appear to avoid nesting in heavily vegetated areas, presumably to increase predator detection (Gochfeld 1984, Martin 1988, Amat & Masero 2004, Muir & Colwell 2010, Saalfeld *et al.* 2011, Anteau *et al.* 2012). However, there are several well-described cases of ground-nesting species from other avian taxa using distraction displays, even when they nest in more enclosed habitats (Wiklund & Stigh 1983, Aragones 1997, Smith 2017, Tseng *et al.* 2017). There are also a few further cases where distraction displays seem effective for birds that are not ground-nesting, including species that typically nest low in trees or shrubs, rock crevices or in holes in trees or walls (Morse 1969, Barash 1975, Burger *et al.* 1989, Leite *et al.* 2012).

The variation seen in distraction display behaviours should be unsurprising given that its wide but patchy taxonomic distribution (Table 1) strongly suggests that it has evolved multiple times. As a relatively low-information signal (c.f. sexual signals, for example), in that nothing particularly complex is communicated to the receiver, this defence can be expected to evolve easily in different species experiencing similar selection pressures. The function of distraction is essentially simply to attract attention, and there are a wide variety of ways in which to do that. Indeed, the novelty of an unusual behaviour may itself help to capture and hold the attention of a predator, leading to selection for diversity. Rather than distraction displays originating from conflicting emotions, as suggested early in the literature (Friedmann 1934), distraction is more plausibly a defence deployed intentionally by adults defending their offspring (Tomkins 1942, Wang *et al.* 2013). The specific behaviours involved probably originate from the displacement or modification of components from other behavioural contexts such as intraspecific aggression or courtship, which distraction displays often resemble at least in part (Armstrong 1949b, Gochfeld 1984). Details of the evolutionary origins of distraction displays remain uncertain (Gochfeld 1984), but certainly the ritualization of new patterns of behaviour based around existing behaviours ought to be comparatively simple for scattered avian taxa to evolve separately given the associated fitness value.

Despite the wide variety of form seen across birds, distraction displays do typically share common features. Often displays demonstrate an re-entrapment element, whereby the parent attempting to distract attention will return to the predator if the predator loses interest (Caro 2014). Adults seem to closely monitor the potential predator by maintaining visual contact whilst performing their displays (Aragones 1997) and modify their own behaviour in response to changes in the predator's behaviour (Ristau 1993). Distraction displays will also usually incorporate transitions between different behaviour patterns and forms of distraction (Gochfeld 1984). Sometimes continuums from one behaviour to another appear to flow unprovoked, and in other cases transitions occur more obviously in response to a stimulus change. On noticing an approaching predator, for example, Kentish Plovers *Charadrius alexandrinus* typically 'crouch-run' to slip away from their nests unnoticed, but if the predation risk persists they then perform more conspicuous displays to distract the attention of the predator (Simmons 1951, Gómez-Serrano & López-López 2017).

Importantly, similarities across distraction displays need not indicate a single origin for the behaviour. Across any cases of independently-evolved distraction, it is reasonable to expect the re-entrapment element of distraction to arise as a displayer must attune its display for its intended audience for it to succeed. Similarly, behavioural transitions are likely to occur during encounters with predators, as flexibility in response to change in predator behaviour is likely to be essential to the fitness value of the distraction behaviour. Such flexibility distinguishes distraction displays from some other forms of nest protection behaviour. If prey sit tight hoping that their crypsis alone defends them they suffer increased risk as a predator approaches, and if they choose to aggressively mob the predator they commit themselves to an attack where they might get injured (da Cunha *et al*. 2017). However, with distraction displays prey can change tactic if necessary. Neither the re-entrapment nor the behavioural transition components compromise the low-information nature or probable ease of evolution of distraction signals from pre-existing behaviours.

Across any taxa where distraction has independently evolved, it is important to note that distraction displays are not always the first line of defence for adults defending young, and there is flexibility in the overall behavioural sequence when disturbed by the presence of an intruder (see Figure 1) (Burger *et al.* 1989, Byrkjedal 1989). Our cost-benefit analysis in this review will explore further which defences will be more effective in different circumstances, but as an anti-predator defence distraction displays will naturally be most effective when individuals are able to use them in a flexible and context-sensitive manner.

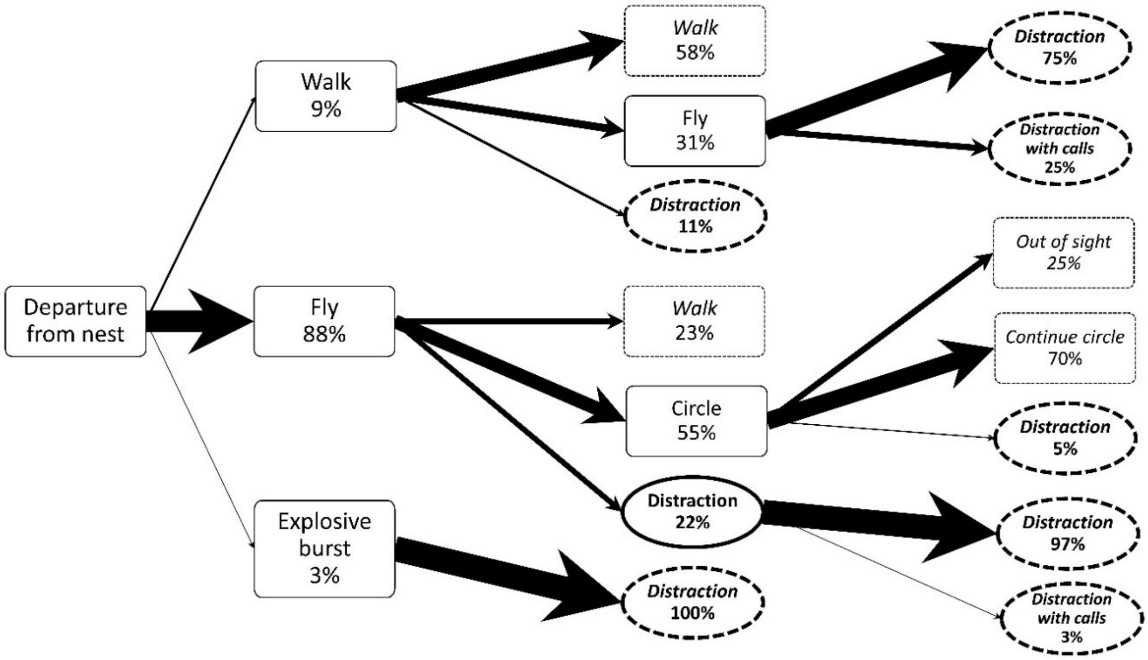

Figure 1: Sequences of behaviour for Zenaida Doves *Zenaida aurita* when disturbed (n = 145), adapted from Burger *et al*. (1989). Distraction displays (circles) can occur at several different points in the defensive sequence. The width of arrows is proportionate to the frequency of the behaviour at that stage relative to the other behavioural options. Italicized behaviours indicate the final activity observed in a given sequence.

Sex differences in distraction display behaviours

The unusually high occurrence of biparental care in birds (approximately 90% of species; Cockburn 2006) makes the variation of parental investment at different stages of parental care an exciting area of research (Kokko & Jennions 2008, Balshine 2012). Sex differences in avian parental care have been reported during nest-building, provisioning and offspring defence activities (Balshine 2012), but distraction displays are rarely mentioned in such broader discussions of parental investment even though diversity in sex roles is found in the distraction display behaviours of many bird species. As is often the case for anti-predator defences, there are numerous examples where the male in a biparental pair carries out the riskier, or in some cases the only, distraction displays (Gochfeld 1984, Brunton 1990, Sordahl 1990b, Yosef 1994, Wang *et al.* 2013). It may be that males perform the riskier parental activities in ground-nesting shorebirds in particular – for whom nest losses are high – because of the importance of females maintaining good condition for production of replacement clutches (Mundahl 1982, Walters 1982, Brunton 1988). The roles of parental care can therefore be partitioned, particularly in monogamous species, so that males and females carry out sex-specific anti-predator behaviours.

However, in many birds, including several non-shorebird examples (Barash 1975, Wiklund & Stigh 1983, Aragones 1997), only females perform distraction displays, although males may defend through more aggressive and potentially even riskier behaviours. Females of precocial species where males adopt sentinel roles may also be more likely to distract if their defence becomes necessary only as risk of nest discovery escalates with increasing proximity of the predator (Pedersen & Steen 1985, Hudson & Newborn 1990). Gómez-Serrano and López-López (2017), however, report that overall use of riskier defence behaviours is greater for female Kentish Plovers than males. This could tentatively be explained by a generally greater investment in reproduction by females (Montgomerie & Weatherhead 1988). A few situations also occur where males and females appear to perform distraction displays with equal vigour (Williamson 1949, 1952).

Sex differences in distraction behaviour across species suggest important differences in parental investment. While there is a wealth of literature on differential parental investment in birds (Owens & Bennett 1994, Møller & Thornhill 1998, Kokko & Jennions 2008, Balshine 2012, Liker *et al.* 2015, Remes *et al.* 2015), distraction displays need to be embedded in that discussion as an important, and obviously risky, form of parental care.

Adaptive value and ecology

Given the striking and varied behaviours, and sometimes differing sex roles, involved in distraction displays, it is important to consider why parents choose to distract and how distraction functions in an ecological context. Clearly, defensive behaviours must play some role in nest survival in order for them to be of adaptive value (Gómez-Serrano & López-López 2017). Partial or full loss of a brood to nest predation could reduce the lifetime reproductive success of a parent, though the extent of this effect will depend on lifespan and re-nesting tendency. So while distracting a predator's attention might place a parent at increased risk of predation, not performing a display and potentially losing a brood could be costly to a parent in a different way (Hudson & Newborn 1990).

The adaptive value of distraction displays lies in their ability to distract or confuse predators. In birds, many flight and running activities, as well as injury-feigning displays, seemingly act to indicate to predators that the performing adult is an easier target to hunt than it normally would be, due to it suffering some form of impediment or being otherwise flight-incapable (Gochfeld 1984). Key to the success of distraction is the fact that not all prey a predator encounters that are behaving as though they are injured are faking it, and a predator that ignored such cues would forfeit easy meals (Ruxton *et al.* 2018). It is reasonable to suggest that on an individual level, local learning should occur. For example, if a predator spends much of its time hunting in an area with many breeding birds exhibiting injury-feigning distraction behaviour, it may change behaviour as a result of prey habituation. However, at a population level, encountering genuinely injured birds may not be unusual for predators as flight is such a fragile ability. Coevolution in response to the deceptive performances of some birds is therefore unlikely in a predator population, as it would also result in predators forfeiting easy quarry. Even if predators in a particular environment did encounter many injury-feigning birds and evolved progressively better discrimination abilities to target truly injured prey while ignoring distracting prey, the prey themselves would in turn be expected to evolve a progressively better ability to convincingly fake injury.

Displacement-type distraction displays differ from injury-feigning in that they do not imply incapacitation; rather they either suggest that no vulnerable eggs or young are in the vicinity as adults appear to be behaving normally or, in the case of false-brooding, that a nest is present far away from the true location of the brood (Gochfeld 1984). Such displays still draw the attention of a predator because their potential (adult) prey appears not to have noticed their presence in most cases and so may be more easily subdued than a wary individual, or may seem to be advertising the presence of vulnerable eggs or young. One particularly interesting displacement-type behaviour – considered by Gochfeld (1984) as a variant of false brooding – does seem to function to honestly advertise vulnerable young to predators, but not the displayer's own. Smith and Smith (1974) described this "nest betrayal" in a Common Ringed Plover *Charadrius hiaticula* which, when approached by an intruder, ran towards a Little Tern *Sternula albifrons* nest and bobbed beside it, seemingly advertising the tern's nest to the predator to distract attention from its own. A similar case was also observed by Gochfeld (1984) in the Least Tern *S. antillarum*. It would be of great interest to know if this behaviour is more common amongst colonial nesters. As with the injury-feigning displays, predators should not be expected to coevolve to ignore displacement-type activities, as such a response would cause them to ignore genuinely easy targets.

The flexible nature of distraction displays as an overall defensive strategy is also key to their adaptive value, with their rapid qualitative and quantitative transitions in behaviour, depending on predator response (Gochfeld 1984). Birds do not use the behaviour when a predator is likely to pass harmlessly by or when the predator is too close to a nest already for the individual to move away undetected (Gochfeld 1984). When deployed, however, the behaviours must successfully attract the attention of predators before they find the nest or are close to chicks. The targeted predators typically possess adaptations that mean they are not easily deterred from found nests and that they are prone to return to discovered nests to plunder them later (Armstrong 1954); preventing this initial discovery thus appears to be the primary goal of parental distraction displays.

Timing during reproduction

For many different forms of parental care, including other anti-predator defences, there is a significant literature on the relationship between parental investment and the stages of reproduction (Amat *et al.* 2000, Currie *et al.* 2001, Post & Götmark 2006, Tarwater & Brawn 2010, Korpimäki *et al.* 2011, Królikowska *et al.* 2016), but the timing of distraction displays specifically as a defence is generally neglected, despite it being an evidently risky type of parental care. Generally, theory predicts that adults should take greater risks when their offspring's reproductive value is highest, and therefore the return expected from the defensive behaviour is greatest (Carlisle 1982). It has long been observed that this is the case in many species of birds (Armstrong 1949b, Skutch 1954), but timing may also be influenced by the relative vulnerability of young at particular ages. The change in frequency of distraction display use over the breeding season (Andersson *et al.* 1980, Burger *et al.* 1989, Brunton, 1990) could be explained by both the 'vulnerability' and 'brood value' hypotheses, the two of which are not mutually exclusive (Onnebrink & Curio 1991).

The vulnerability hypothesis suggests that the intensity of nest defence, including distraction displays, increases with the vulnerability of offspring to predation (Burger *et al.* 1989, Brunton 1990). For altricial bird species, vulnerability should be high from hatching until fledging, as young are unable to defend themselves (Burger *et al.* 1989). Older nests are typically more conspicuous as young beg for food louder and are fed at a higher rate, and additionally older offspring are more profitable to predators due to nestling growth (Greig-Smith 1980). Consequently, nest defence may increase with nestling age, peaking immediately prior to fledging, concomitantly with chick vulnerability (Barash 1975, Brunton 1990). Specific to distraction, several studies suggest that altricial birds do indeed show the most intense displays at the end of the nestling period (Armstrong 1956, Barash 1975, Andersson *et al.* 1980, Greig-Smith 1980, Leite *et al.* 2012). For precocial bird species, offspring survival potential increases rapidly after hatching with mobility improving significantly over a matter of days (Barash 1975). Parental defence should consequently increase immediately post-hatching, but then gradually decrease up until the point where the offspring can protect themselves (Barash 1975, Brunton 1990). Several studies have found supporting evidence where precocial birds perform distraction displays most intensely around hatch date and over the immediate few days afterwards (Simmons 1955, Stephen 1963, Gramza 1967, Tseng *et al.* 2017).

The brood value hypothesis, on the other hand, predicts that defence levels and risk-taking by parents should increase as the fitness value of young increases (Patterson *et al.* 1980, Winkler 1987, Montgomerie & Weatherhead 1988, Redondo & Carranza 1989, Jukkala & Piper 2015). Typically fitness value increases with age as young are more likely to survive to reproductive age (Patterson *et al.* 1980). Smith and Wilson (2010) found that nest defence behaviour shown by biparental shorebirds intensified as nests aged and the breeding season progressed, supporting the brood value hypothesis, but this pattern was not seen in uniparental species. However, few empirical studies have tested the vulnerability and brood value hypotheses in the context of distraction behaviour specifically, and most of these have provided more support to the vulnerability hypothesis (Burger *et al.* 1989, Brunton 1990, Hudson & Newborn 1990). It must be noted, though, that for some birds both hypotheses would predict greater defence – including distraction – as the young grow progressively older. As noted above, several altricial birds show the most intense displays at the end of the nestling period when their chicks are most vulnerable, but at this late stage in the breeding season there is also less time to lay a replacement brood, so it is worthwhile parents investing greater defences in their current brood. For many altricial species, therefore, the brood value and vulnerability hypotheses may be indistinguishable in their predicted effects.

In some cases, the empirical evidence of distraction display behaviour does not yet clearly accord with either the brood value or vulnerability hypotheses. For example, Pedersen and Steen (1985) found that the intensity of distraction display use by precocial Willow Ptarmigan *Lagopus lagopus* was high up to the time when the chicks were a few days old, as predicted by the vulnerability hypothesis, but remained undiminished for at least three weeks post-hatching. This sustained intensity of distraction is contrary to other precocial birds (such as waders and ducks) and does not follow the typical pattern predicted by the vulnerability hypothesis. However, the authors suggested that this may be due to a later age of thermoregulatory independence in young ptarmigan, which could mean the parental behaviour does therefore correspond with at least one, if not both, hypotheses. While this suggestion needs to be tested, future quantification of variation across a grouse breeding attempt in other forms of parental care would help explain such unusual persistence of distraction displays (Hudson & Newborn 1990).

Distraction display occurrence and intensity can also vary during nest-building and incubation. For example, distraction displays are slow to mature in incubating Eurasian Oystercatchers *Haematopus ostralegus*, and become more proficient towards hatching (Williamson 1952). In the Arctic Skua *Stercorarius parasiticus*, entirely different variations of broken-wing display are performed early in the incubation period compared to later when the eggs are close to hatching or there are young at the nesting ground. Earlier on, the display involves the parent leaping up and then crouching and flapping while fairly stationary on the ground, while once eggs are closer to hatching the lure display involves more vigorous wing-thrashing and is more likely to be accompanied by vocalisations (Williamson 1949). Tseng *et al.* (2017) draw attention to studies that demonstrate how the timing of injury-feigning behaviours also varies among species of nightjar (Caprimulgidae). Swamp Nightjar *Caprimulgus natalensis* and Blackish Nightjar *Nyctipolus nigrescens* males display injury-feigning behaviour during incubation (Ingels *et al.* 1984, Hustler & Mitchell 1997), whereas the Savanna Nightjar *C. affinis* (Tseng *et al.* 2017) and Freckled Nightjar *C. tristigma* injury-feign only during the nestling period (Steyn 1971).

For the Blackish Nightjar the eggs are the most vulnerable developmental stage, corresponding with the timing of most frequent distraction display use (Ingels *et al.* 1984). It is reasonable to suppose that the behavioural differences found in the timing of distraction displays reflects the differing predation risk during each stage of the nesting period for different species (Tseng *et al.* 2017). For all bird species, future comparative studies exploring the timing of distraction displays (Sordahl 1986) in relation to ecological factors such as predation, will provide valuable insights into the evolution of these behaviours.

Conditions for the evolution of distraction

Distraction displays vary in their form, timing, and occurrence across bird taxa, but what are the conditions that make the evolution of distraction likely? Answering this question is essential to understanding the sparse occurrence of the behaviour across taxa, despite its apparent adaptive value in the contexts in which it is found. The fitness value of distraction display is likely to be greatly reduced if the decoy individual is unable to quickly escape a predator, for example by flight, and this may explain why distraction displays are most prevalent in birds. This being the case, the predators against which distraction is most effective would be expected to be ground-based (Armstrong 1954). Considering the prey individuals, their predators, and their location, Armstrong (1954) outlined six factors which may predispose birds to use distraction displays:

1. The nest or hiding place of the young is on open and exposed terrain, allowing a parent to detect a predator before the predator has detected the offspring (Dyrcz *et al.* 1981, Amat & Masero 2004, Muir & Colwell 2010, Anteau *et al.* 2012, Gómez-Serrano & López-López 2014), attract its attention and lead it away; the many species of shorebirds that favour predator detection over nest crypsis in nest site selection (Götmark *et al.* 1995, Gómez-Serrano & López-López 2014) fulfil this requirement;
2. The nest is accessible to non-avian predators, typically on or near the ground;

3. The nest is inconspicuous, such that it would not be obvious to a predator and a parent's distraction behaviour could prevent detection, and/or insubstantial structurally, such that neither material nor additional fortification from its surroundings serves to protect the young within;

4. The prey bird does not nest colonially, so that a parent's territory is large enough that the finding of another's nearby nest by a predator does not facilitate the discovery of its nest, except in so far as the experience may improve the predator's ability to search for and detect nests;

5. The main predation threat is diurnal, as elaborate distraction need to be visible to the predator;

6. The bird breeds in higher latitudes with extended daylight, where diurnal predation risk predominates.

To summarise, distraction displays should be the most advantageous for birds with inconspicuous nests in vulnerable situations that are exposed to predation by diurnal, ground-based predators (Armstrong 1954). In situations where these conditions exist and given the low-information nature of distraction displays, it should be relatively easy for distraction display patterns of behaviour to evolve from a base of similar behaviours used for different functions.

Cost-benefit analysis

Assessing the costs and benefits of any animal behaviour relative to the suite of possible behavioural options available is a valuable framework in which to consider its expression, utility and consequences in any given ecological context. Here, we conduct a cost-benefit analysis of distraction displays compared to the use of alternative anti-predator tactics in different situations that prey may encounter.

Benefits

The obvious benefit of anti-predator distraction displays for adult birds is the defence of their young (Gochfeld 1984, Smith & Wilson 2010, Gómez-Serrano & López-López 2017). Offspring survival translates into increased reproductive success and overall lifetime fitness for the parents. As discussed earlier, the timing of the occurrence and frequency of displays varies between bird species, apparently dependent on how and when the behavioural strategy best maximises return on parental investment (Barash 1975). Distraction displays clearly serve a useful anti-predator function in some bird species, but otherwise it is not common behaviour. The potential costs associated with the behaviour go some way to explain this pattern across taxa, and it is these costs which we consider in more detail.

Costs

For all species that use distraction there will be associated energy costs, particularly where the display is elaborate and continues for a long time through various transitions over long distances as the individual attempts to lead predators away. Time spent distracting predators is also less time spent feeding, incubating, or maintaining nest structures, and so individuals may have to expend further energy in the immediate aftermath of distracting predators in order to compensate (Montgomerie & Weatherhead 1988, Gómez-Serrano & López-López 2017). Distraction behaviour may thereby reduce fitness, though such long-term reproduction or survival costs of distraction displays would be difficult to accurately quantify.

Fitness costs if displays inadvertently provide a clue to the location of offspring will be more severe and more easily quantifiable then energetic costs (Gochfeld 1984). This cost may not necessarily be associated with the focal predator that the original display was intended to attract. More eye-catching displays, for example, could unintentionally attract other predators that may then pursue the adult or start searching for their young nearby. Gochfeld (1984) also drew attention to an observation by Matthiessen (1967) that the re-entrapment practices by shorebirds after performing a “rodent run” distraction behaviour represents a vulnerability, as predators may recognise from their prey’s pauses that they are not in fact dealing with a fleeing rodent. The re-entrapment behaviour essential to responsive and flexible distraction displays may be a weakness in other distraction behaviours too, and such predator-monitoring pauses may be used as a clue to trigger predators to abandon interest in the parent and return to search the vicinity for young (although we know of no empirical exploration of this suggestion).

Considering the environments in which distraction displays are most common, further costs can arise. Because distraction displays are frequently associated with comparatively open nest locations, with unimpeded views of the surroundings so that predators are detected by parents as they approach (Armstrong 1954, Gochfeld 1984, Muir & Colwell 2010), birds occupying such locations may experience higher thermoregulatory costs due to factors such as increased wind speeds, particularly in arctic environments. Parents and their offspring at open nest sites may also be more susceptible to threats that do not respond to distraction displays, such as avian predators.

In the uncommon scenario where predators find themselves responding to distraction displays more commonly than they encounter genuinely-injured prey, there is an alternative risk of predators becoming habituated to such displays. Sonerud (1988) reports two encounters between brood-attending grouse hens (Tetraonidae) – a black grouse hen *Tetrao tetrix* and a capercaillie hen *T. urogallus* – and a Red Fox *Vulpes vulpes* where the fox appeared to ignore the distraction displays of the hens and instead changed its behaviour in a way that was interpreted as enhanced searching for a nest. In circumstances such as this, where local learning may have occurred for a predator with several breeding prey in its territory, the conspicuousness of distraction displays carries the risk of further attracting a predator's attention to offspring.

Beyond potentially informing a predator of offspring presence, distraction displays can also carry a risk of predation for the parent themselves. Self-sacrifice would likely also be fatal to a parent's dependent young so the fitness cost is likely to be total, but birds exhibiting distraction displays do occasionally get captured during distraction efforts (Gochfeld 1984, Brunton 1986, Sordahl 1990a, Amat & Masero 2004, Gómez-Serrano & López-López 2017). While some of these cases do involve the bird being captured by the predator to whom the display was directed (Brunton 1986, Sordahl 1990a), there are a couple of observations that have involved displaying birds being preyed upon by raptors, such as a Montagu's Harrier *Circus pygargus* (Amat & Masero 2004) and a Common Kestrel *Falco tinnunculus* (Gómez-Serrano & López-López 2017). In these latter cases, displays were most likely to have been deployed against other predators, but the raptors were able to opportunistically predate the birds while they were engaged in distraction behaviour. The importance of all captures during distraction displays should certainly not be neglected in considering the potential costs of this behaviour (Brunton 1986, Lima & Dill 1990, Sordahl 1990a, Gómez-Serrano & López-López 2017). For all species that employ distraction display behaviours there is likely some risk of capture by the predator to which the display is aimed, as predators are evolutionary disposed to not ignore signals suggesting an easy meal (Ruxton *et al.* 2018). However, many observations suggest that individuals engaged in defence are constantly alert, probably even in a state of hyper-alertness (Gochfeld 1984). Fatal outcomes for prey are expected to be rare because otherwise selection would act strongly to eliminate such a high-risk behaviour (Gochfeld 1984, Gómez-Serrano & López-López 2017).

Different levels of risk are likely to be experienced by birds performing different types of display. While there is little quantitative evidence, some studies suggest that birds performing riskier displays gain a greater reward from the behaviour. For example, Byrkjedal (1987) found that ground-based distraction displays, which suggest a high degree of incapability but also make the displaying parent relatively vulnerable, were more efficient and had a greater effect on nest survival than displays performed while flying away from the nest. Further, the findings of Gómez-Serrano and López-López (2017) also suggest that the longevity of nests can be greater when parents take greater risks as part of their distraction display behaviour. Certainly, investment in anti-predator defence should be proportional to predation risk (Lima & Dill 1990) and flexible according to the specific circumstances.

We next consider the trade-offs involved in distraction displays, and what situations may provoke distraction in preference to alternative anti-predator tactics.

Trade-offs and alternative tactics

Prey characteristics

Many factors can influence the effectiveness of avian distraction displays and whether they are likely to be used against predators instead of other tactics. First, prey characteristics will affect propensity to use distraction displays, including interspecific variation, individual variation, spatial variation (geography and populations), temporal variations (within seasons and over lifespans), sex, size, and habituation and learning (Gochfeld 1984). Interspecific variation is exemplified well by three closely-related plover species which vary in the timing and style of distraction displays (Simmons 1953). The Little Ringed Plover *Charadrius dubius*, the Kentish Plover and the Common Ringed Plover show similarities in form and performance of displacement-type activities, crouch-runs and stationary distraction displays, but each species has its own distinctive style for the various behaviours (Simmons 1953). A display which is common in one species can also be much rarer in the others, for example, the Little Ringer Plover has a notable impeded-flight distraction display which is not shown in well-developed form in the other two species. Although closely-related, therefore, these three plovers presumably face different trade-offs that have shaped the evolution of their anti-predator behaviours. Within a species, Williamson (1952) provides an excellent account of regional variation in the distraction displays of Eurasian Oystercatchers, as forms of distraction are frequent and elaborate in oystercatchers on the Faeroe Islands but are apparently very rare among the oystercatchers of the British Isles and adjacent parts of Europe. Further evidence of individual variation is found in the Kentish Plover. Gómez-Serrano and López-López (2014) studied birds that frequently performed distraction displays to lure human observers away from nest sites, but in another relatively nearby population of the same species Amat and Masero (2004) found that birds did not perform distraction displays towards humans. It seems that there may therefore be intrapopulation variation in whether certain predators are targeted by distraction displays, in addition to the individual variation that can be found in the occurrence, frequency and intensity of distraction displays against the same stimulus.

The seasonal timing of distraction displays and the influence of sex on distraction behaviour have been discussed earlier, but sex differences can also relate to size differences in the individuals that distract (Wiklund & Stigh 1983). Considering temporal influences, Tseng *et al.* (2017) found that older female nightjars injury-feigned more often than younger conspecifics, suggesting that while the individual's residual reproductive value declines with age, maternal experience in brood defence increases (Montgomerie & Weatherhead 1988). Broods may be more valuable to experienced parents, whose defence has improved over time so that there is a reduced cost associated with challenging predation threats (Tseng *et al.* 2017). As well as experience, prey habituation can impact the frequency of distraction displays. Lord *et al.* (2001) found that distraction display intensity of North Island New Zealand Plovers *Charadrius obscurus aquilonius* was unrelated to various approach types by humans (walking, running, or leading a dog), evidencing habituation to humans on busy beaches. Other studies have also found evidence for greater habituation to humans in multiple bird species occupying areas of higher human disturbance compared to those in low disturbance areas as flight initiation distance varies, suggesting that birds are capable of adjusting anti-predator response to the disturbance level experienced (Ikuta & Blumstein 2003, Gómez-Serrano & López-López 2014). Interestingly, St Clair *et al.* (2010) showed that not only do Two-banded Plovers *Charadrius falklandicus* show decreased flushing distances in response to humans in areas where human activity is high, but they also conversely show increased flushing distances in response to humans in areas where mammalian predators (Feral Cats, *Felis catus*) are present. This second finding suggests generalization or sensitization of the birds to potential predators, implying that introduced mammalian predators can increase the effects of non-lethal human disturbance on plover fitness (St Clair *et al.* 2010).

Individuals' capacities for other defensive tactics, such as crypsis or mobbing, may also influence how attractive distraction displays are as an option to prey within given situations. Certainly, the behaviour should be suppressed in favour of another if the predator has approached so closely that the defending bird could not leave its nest undetected before initiating a display (Gochfeld 1984, Ruxton *et al.* 2018). When performing, the closer a parent is to a potential predator, and the more intense its display, the greater the risk compared to other behaviour (Brunton 1990, Lima & Dill 1990) and so assessing predator proximity will be an important component of any decision to distract. Recently, Smith and Edwards (2018) found that individual White-rumped Sandpipers *Calidris fuscicollis* and Red Phalaropes *Phalaropus fulicarius* that flush from their nests at long distances in response to approaching threat leave the vicinity of the nest immediately, while those that flush from close distances are more likely to engage in injury-feigning. This latter strategy was associated with reduced risk of nest predation, but long-distance flushing may be less common due to these birds' concealed nest sites (Smith & Edwards 2018). Certainly, degree of nest concealment can be expected to influence individual variation in flushing distance and the co-occurrence of additional defensive behaviours. Gómez-Serrano and López-López (2014) demonstrated that the distance at which Kentish Plovers flushed decreased with vegetation cover, highlighting how more conspicuous (exposed) individuals might be able to compensate for a higher predation risk by modifying their anti-predator behaviour, in this case by flushing earlier.

Predator characteristics

Characteristics of the approaching intruder should also be expected to influence the trade-offs surrounding distraction displays (Gochfeld 1984). Predator type, for example, is an important determinant of American Golden Plover *Pluvialis dominica* defensive behaviours as the birds show markedly cryptic responses to avian predators but give distraction displays in response to the approach of ground predators (Byrkjedal 1989). These different behaviours could result from differences in diurnal activities of avian and ground-living predators. The more visually-oriented avian threats operate during the day, and so would be attracted by conspicuous movements, whereas many ground predators of this species are crepuscular (Byrkjedal 1989). Other studies support similar discrimination of predator type and resultant selection of the most appropriate anti-predator response (Walters 1990, Clemmons & Lambrechts 1992, Sordahl 2004); cryptic behaviour and aggressive mobbing are more commonly deployed against avian threats, while distraction displays are more commonly deployed against terrestrial threats. If a bird's predator is also flight-capable, flight will no longer be an easy escape option for distracting parents when they themselves become the target of attacks. Prey individuals should discriminate among predators based on both the risk to the adult in performing a given defensive behaviour and the risk to the offspring in not doing so, relative to the alternative tactics available to the parents.

A predator's size can also be an important characteristic that influences the propensity of its prey to show distraction behaviour. Red-crowned Cranes *Grus japonensis*, for example, will attack non-human intruders such as dogs, Hen Harriers *Circus cyaneus*, and Pied Harriers *C. melanoleucos* and drive them away from their nest without showing injury-feigning behaviour, but respond to the approach of a human by injury-feigning (Wang *et al.* 2013). The authors interpret this as resulting from humans being much larger than the other intruders. Of course, not all birds confidently drive away such a range of potential predators and indeed there are several examples of birds using distraction displays against intruding dogs (Amat & Masero 2004, Gómez-Serrano & López-López 2014, 2017). Armstrong (1954) noted that birds seldom injury-feign to threatening stimuli smaller than themselves but that there are cases which demonstrate that there cannot be assumed to be a direct relationship between larger predator size and the tendency to injury-feign. The manner in which an intruder approaches and responds to initial distraction attempts should also be expected to influence whether a display is started or continued by prey (Armstrong 1954, Blumstein, 2003).

Environmental characteristics

Contextual characteristics such as habitat and weather will also affect the benefits and costs of distraction displays (Gochfeld 1984). While distraction behaviour is typically selected for in open environments, prey that use distraction displays may still occupy habitats varying in vegetation and potential nest cover. As an example, Savanna Nightjars display injury-feigning more frequently in low-plant-cover habitats, where predators might have detected their broods more easily (Tseng *et al.* 2017). Similar relationships between the degree of nesting cover and distraction display intensity have been found in Red Grouse *Lagopus lagopus scotica*, whose display intensity is negatively correlated with vegetation height (Hudson & Newborn 1990), and in American Robins *Turdus migratorius*, whose extreme distraction displays are more common in parents with poorly concealed nests than in those with well-concealed nests (McLean *et al.* 1986). However, the interplay between nest location and thermal stress can complicate this trend. Gómez-Serrano and López-López (2017), for example, found that Kentish Plover males and females nesting in concealed sites invested twice as much in nest defence (behaviours involving leaving the nest) compared to those nesting in exposed sites. The authors suggest that this apparent contradiction may explained by the fact that the exposed nests were in unvegetated beach areas exposed to the sea breeze, which may have a thermoregulatory effect that alleviates heat stress on eggs and the incubating adult. By contrast, the concealed nests might experience higher temperatures and consequently be more vulnerable to egg or embryo loss while incubating adults are absent for a prolonged amount of time. Birds nesting in concealed sites may therefore have performed more intense and risky distraction displays in order to move the predator away as soon as possible, thus avoiding egg loss to overheating (Gómez-Serrano & López-López 2017). However, prey characteristics can also be important to the relationship between distraction displays and these environmental characteristics. Birds that breed in more exposed areas may often be found to have a better body condition than those that breed in the least exposed places, presumably because they can better cope with the heat stress imposed by exposed locations (Amat & Masero 2004).

Temperature has also been found to influence nest return times following an anti-predator distraction display. For example, at very high temperatures Malaysian Plovers *Charadrius peroni* return to their nests quickly, regardless of how old the embryos inside their eggs are (Yasué & Dearden 2006). The risk of heat stress may outweigh parental investment decisions on distraction displays (Yasué & Dearden 2006), as parents cannot always risk leaving their eggs unattended despite the threat of predation. Post-distraction nest return times may also be influenced by weather variables such as rainfall or small-scale differences in wind speed around nests (Zerba & Morton 1983, Yasué & Dearden 2006). Beyond creating a need to return to incubation, it is certainly reasonable to suppose that weather variables such as strong winds and heavy rainfall may also limit long-range predator identification. In itself, reduced detection capability may affect how viable distraction displays are, depending on whether predators have been able to approach closely undetected or not.

Sociality

An additional consideration associated with the trade-offs of distraction is the sociality of birds. Some birds breed near other breeding pairs and this may influence frequency of particular anti-predator defences. Colonial species are far less likely to engage in distraction displays than solitary nesters (Gochfeld 1984), instead tending to aggressively mob or 'scold' intruders, or take advantage of protective "umbrella" species' aggressive defence (Larsen & Moldsvor 1992, Smith *et al.* 2007, Cervencl *et al.* 2011). Some species that nest colonially do use distraction behaviours in groups though, such as the Arctic Skua, and in these cases mutual stimulation can pass the pattern of behaviour through the colony so that multiple pairs perform distraction displays at once (Williamson 1949). Mutual stimulation may cause behavioural patterns to mature much earlier in colonial than in solitary pairs, perhaps leading to more effective anti-predator defence developing earlier in the breeding season and increased brood survival (Williamson 1949).

The decision to use distraction displays against predators is clearly dependent on many factors, relating to the prey, their predators, the context and, in some cases, the sociality of the prey. Given the large number of influencing variables, the flexibility of distraction displays is likely to be an important aspect of their effectiveness in species in which they have evolved. It is advantageous for prey to use several different behavioural strategies depending on specific circumstances (Meltofte 1977, Sordahl 2004) and it should be expected that the behaviour will vary. Following observations of foxes ignoring distracting grouse hens, Sonerud (1988) constructed a game theory model to predict when distraction display would be more profitable to adult birds than just flying off. A greater abundance of rodents, on which foxes also feed, in one year might result in higher birth rates in foxes and, therefore, a greater population of one-year-old foxes in the subsequent year. Young foxes' inexperience in predation of grouse may make distraction displays a profitable strategy for grouse in the years following a boom in the rodent population. Conversely, if there is a low rodent population in a given year, grouse in the following year may better protect their offspring by not using distraction displays, as they are more likely to encounter experienced, older foxes. The frequency of distraction displays towards foxes in brood-attending hens might be predicted to vary, therefore, depending on both the experiences of the predators and the prey. The predictions of this model provide a good example of how the broader ecology of systems (in this case previous availability of other prey to focal predators) may need to be considered to truly understand what guides the decision to use anti-predator distraction displays. Empirical evidence of the behaviours of brood-attending willow ptarmigan hens supports the idea of there being fluctuating benefits to distraction displays based on the demographic structure of predator populations (Pederson & Steen 1985), but it would be difficult for empirical studies to quantify whether parent birds adjust the frequency of distraction displays according to their likely success against predators against a background of long-term demographic changes (Sonerud 1988).

Distraction displays in non-avian taxa

As a form of parental care, distraction display behaviour is necessarily restricted to those taxa that invest in such strategies. Even in some taxa, such as mammals, where parental care may be present distraction displays might not be necessary; for example, large mammals will often defend their young through aggression, while some smaller mammals instead conceal their young in burrows. Without the conditions outlined above, such as an inconspicuous but exposed nest and parents that are attractive to predators but also able to rapidly evade them, distraction displays are unnecessary or too costly a defence. Birds are without question the most prominent taxa which meet these criteria, but there are a few cases of distraction displays that have independently evolved in other taxa. Considering these other cases helps to understand the conditions that are essential for distraction to evolve and why it is most common in birds.

Intriguingly, considering the great difference in lifestyles and environment, the most well-known non-avian case of distraction behaviour has been reported in a species of fish. Three-spined Stickleback *Gasterosteus aculeatus* males show uniparental care and guard nests containing their eggs (Fitzgerald & Wootton 1986). When approached by a group of conspecifics, who may attempt to raid nests to cannibalise eggs, male sticklebacks use distraction displays to deceive the group and decoy them away from the nest (Whoriskey & Fitzgerald 1985, Foster 1988, Ridgway & McPhail 1988, Whoriskey 1991). While other species of fish defend highly visible algal mats (Barlow 1974, Robertson *et al.* 1976, Foster 1985) or brightly-coloured egg masses (Foster 1987), sticklebacks' nests are not readily detectable to conspecifics. Foster (1988) suggests from this that distraction displays are, as in birds, unlikely to be effective when young are conspicuous and easily detected by predators (Armstrong 1949a, Skutch 1954). Distraction can include a 'show' of conspicuous behaviours (Whoriskey 1991) or false-rooting (i.e. false feeding) displacement-type behaviours, where the male apparently mimics foraging away from his nest (Ridgway & McPhail 1988, Whoriskey 1991). If the male's distraction display is successful, the approaching conspecifics join him and attempt to feed nearby rather than continue to approach his nest (Whoriskey & Fitzgerald 1985, Foster 1988, Ridgway & McPhail 1988, Whoriskey 1991).

Distraction in sticklebacks markedly differs from in birds in the difference in risk to the defending parent (Foster 1988). For birds, distraction displays bring predation risk to the performer. Stickleback adults, by contrast, are not vulnerable to predation by conspecifics and so their tendency to perform distraction displays is influenced only by the probability of success in defending their young (Foster 1988). However, as happens occasionally to birds, parents may unintentionally attract the attention of other stickleback groups to their offspring, particularly during more elaborate displays (Foster 1988). Distraction displays could also be costly for stickleback males when cannibalistic groups are already in the territory because movement near the nest can alert the group to its presence (Foster 1988). As in birds, distance has been proven to be important to sticklebacks' assessment of risk and subsequent performance, as their showier distraction display is executed when intruders are closer and the threat to nest survival is presumably the greatest (Whoriskey 1991). The simpler 'rooting' display seems employed only to steer away groups that are outside, but heading towards, the male's territory (Whoriskey 1991).

Distraction displays have also been recorded in two mammal species defending their young. Long (1993) reported an American Red Squirrel *Tamiasciurus hudsonicus* mother performing a conspicuous display in response to an approaching human, including repeated fleeing and returning movements in combination with a bivocal call, that appeared menacing while also resembling cries of nearby young. Long describes this behaviour as obviously serving as a nest-site distraction to lessen predation on young red squirrels when they are especially vulnerable. Squirrels are small mammals with nests that are inconspicuous but exposed, and so provided that a squirrel can escape rapidly, which is likely given its agility, it does fulfil the main conditions where distraction displays could evolve. However, even where offspring are mobile, there is some evidence of mammals using distraction displays to defend their young. Adult male Mentawai Langurs *Presbytis potenziani*, perform what have been interpreted as distraction displays in response to approaching humans (Tilson & Tenaza 1976). The display consists of branch bouncing and loud vocalisations as the male runs through the canopy; meanwhile the male's female partner and immature young hide silently and motionless in the canopy. It is, however, perhaps difficult to determine whether this is truly distraction behaviour or more a form of intimidation or signalling of perceptual awareness. It could serve multiple functions, but understanding is necessarily limited by the behaviour only being described in response to humans; we cannot yet say whether natural predators might switch their focus to the displaying individual.

Beyond the rare examples described above, there are perhaps unlikely to be many more cases where non-avian taxa use distraction displays to defend their young. For distraction displays to be effective, the prey needs to be able to advertise itself as an easy target that would lure a predator but also have a means by which it can ensure it does not actually become an easy meal; the ability to fly is the most obvious and effective way to have such an advantage where a predator is not flight-capable.

Conclusions and outstanding opportunities for future research

Distraction displays encompass some of the most dramatic parental care behaviours found in nature, and here we have offered a new definition that seeks to unify research spanning the great variety in form that distraction can take. We hope that, alongside this definition, our much-needed review of the field of distraction displays will provide both an updated synthesis of what is known about the defence in birds and provide a solid starting-point to inspire further studies. Perhaps because of the extravagance of some of the displays, the field of distraction has consisted primarily of descriptive reports to date. However, we believe that increased quantification of distraction displays within a behavioural ecology framework will allow for significant advances in our understanding.

Distraction displays are found in a several avian taxa, but primarily shorebirds. Through examining the variation in the form and occurrence of distraction behaviour between sexes, at different times of birds' reproductive cycles, and across a range of different ecological circumstances – as this review has sought to demonstrate – we can further understand the importance of its flexibility and the trade-offs central to its effectiveness. Despite costs associated with it, distraction can be an advantageous anti-predator tactic for parents defending young, but we suspect that distraction displays do not occur so often in nature compared to other defences. The fact that most cases of distraction behaviours have been recorded in avian taxa is unsurprising, as the fitness value of the behaviour would be greatly reduced if the displayer cannot quickly escape out of a predator's reach (Armstrong 1954).

Correspondingly, distraction displays will be most common where the main predator is ground-based, such that it cannot give chase by flight or rapidly climbing trees, and where it is diurnal (Armstrong 1954), as the displays need to be primarily visual so that the predator can localise the source of the display precisely. Additionally, in an environmental context, distraction displays are most commonly found in open, exposed habitats such as shores (Armstrong 1954), which allow for distant detection of the predator and distant performance of the display from the offspring.

To summarise, we suggest that distraction displays are rare due to the necessity of:

1. the individual acting as decoy having some means by which to rapidly evade capture that is not obvious to potential predators (or not 100% effective against them),
2. the main predator targeted typically being ground-based and diurnal (and able to predate both parents and offspring),
3. the habitat typically being open and exposed, and
4. the nest containing eggs or young to defend will usually be relatively hard to find, in order for distraction displays to keep its location hidden, but will also offer no physical protection itself, as broods would almost certainly be destroyed were predators successful in locating it.

The most important of these is probably the first, as the long-term costs of predation for the defending adult would make the behaviour maladaptive otherwise, but this 'rapid-escape-measure' is not a quality that most species possess. There are, of course, exceptions to all these potential ecological drivers for the behaviour, but they provide some framework for the limitations of distraction displays as an anti-predator defence and highlight the importance of understanding the different contexts in which distraction appears to be used.

To better understand the evolution and behavioural ecology of distraction displays in birds, we suggest that comparative studies within and between species will be most valuable when they explore the timing and occurrence of distraction displays in relation to a range of ecological factors. As an over-arching suggestion for future research, we recommend exploring distraction displays through a behavioural ecology cost-benefit framework, quantifying behaviours and the trade-offs that prey species will experience. As high-energy and often high-risk behaviours, the costs of distraction displays can only be compensated for when the likelihood of survival and the investment defended is high enough. All predation threats faced by a prey species should be fully evaluated in terms of types of threats in the locality (e.g. ground or avian) and their respective magnitudes. We might predict that distraction displays will be used when a solitary ground-based predator is approaching a bird's nest for example, as the parent will be able to distract it and successfully escape. But if the cost of attracting more nearby predators by using a display – perhaps opportunistic avian threats to which distraction displays are not usually targeted (Amat & Masero, 2004, Gómez-Serrano & López-López, 2017) – is likely to increase the threat to its young, or itself to a substantial degree, then an alternative anti-predator defence may be most advantageous.

There remains much still to be discovered about the role of various individual characteristics in determining how and when birds use distraction displays, and so we recommend further empirical studies explore variation in distraction within species. Sex, age and experience have been demonstrated to be important in the frequency and quality of distraction displays in some species (e.g. Tseng *et al.* 2017), but it would valuable to learn how characteristics such as size, condition and even colouration may influence how birds use distraction compared to other defensive strategies. If a bird is in excellent condition it may have the size, strength and energy for distraction displays or effective aggressive defence, while individuals in poorer condition or perhaps with more effective colouration may opt for crypsis with its far lower energetic cost. Quantification of the energetic costs of distraction displays and subsequent fitness consequences for parents would be of enormous value here, but large datasets would be needed to compare the performance of individuals from a spectrum of 'distraction behaviour use' while accounting for their specific ecological context. Intraspecific interactions may also be useful to quantify where populations of breeding birds are likely to encounter conspecifics. Williamson's (1949) work described the mutual stimulation of distraction displays in Arctic Skus, while Bomford (1986) found that a displaying Banded Dotterel *Charadrius bicinctus* immediately ceased displaying on the approach of a conspecific and moved away. The likelihood of predators coming across nests and the degree of intraspecific sociality perhaps interact to influence individuals' propensity to engage in distraction behaviours.

Habitat variables, such as plant cover (Metcalfe 1984, McLean *et al.* 1986, Hudson & Newborn 1990, Amat & Masero 2004, Gómez-Serrano & López-López 2014, Tseng *et al.* 2017) should also be considered in weighing the costs and benefits of distraction displays, as the physical environment around a nest will have an important influence on how well-concealed or detectable are a parent's young. Including records of environmental conditions, such as temperature (Yasué & Dearden 2006), rainfall and wind (Zerba & Morton 1983), could also increase awareness of prey's long-range predator detection and the costs to young of parents remaining away from a nest during distraction (e.g. thermal stress on eggs, see for example Weston *et al.* (2011)), helping to explain the occurrence and duration of distraction displays in some species.

Developing studies that will help disentangle the costs and benefits of distraction displays during longer-term encounters between predators and their prey could also be insightful, particularly where there is a risk of delayed nest predation. If predators are able to remember a nest's position when the parents are incubating they may be able to predate the nest when the parents are away (Salek & Zamecnik 2014). It would be interesting to find out whether the distractive efforts of adults are ignored by predators in some situations because of prior knowledge of a nest's location, rather than the display itself acting as a cue to the presence of a nearby nest. To further unpick the sex differences sometimes found in distraction displays, we also suggest that further studies should seek to explore the links between parental investment and behavioural dimorphism between sexes across a range of species. Additionally, while reactions to humans can be considered as comparable to reactions to other ground predators (Armstrong 1956), more observations of natural predation would be valuable, perhaps with the help of remotely-controlled cameras. This is particularly important where a potentially distractive function of a behaviour needs to be distinguished from intimidation or signalling of perceptual awareness.

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Table 1: The major categories and sub-categories of anti-predator distraction display used by birds as part of offspring defence, as classified by Gochfeld (1984), with some example species and references from Gochfeld's chapter and more recent work.

Categories	Sub-categories	Example species	References
Standing still	**Alert postures**	Western Sandpiper, *Calidris mauri*	Brown (1962)
	Head-bobbing	Kentish Plover, *Charadrius alexandrinus*	Simmons (1951)
	Tail-flagging	Magellanic Oystercatcher, *Haematopus leucopodus*	Miller and Baker (1980)
Flying activities	**Explosive departure**	Zenaida Doves, *Zenaida aurita*	Burger *et al.* (1989)
	Impeded flight	Black-throated green Warblers, *Setophaga virens* Eurasian Woodcock, *Scolopax rusticola* Golden-crowned Warbler, *Basileuterus culicivorus azarae*	Morse (1969) Lowe (1972) Smith (2017)
	Diversionary circling	Eurasian Oystercatcher, *Haematopus ostralegus* Buff-breasted Sandpiper, *Calidris subruficollis* American Avocets, *Recurvirostra americana*, and Black-necked Stilts, *Himantopus mexicanus*	Williamson (1952) Sutton (1967) Sordahl (2004)
Running activities	**Crouched run**	Kentish Plover, *Charadrius alexandrinus* American Avocets, *Recurvirostra americana*, and Black-necked Stilts, *Himantopus mexicanus*	Simmons (1951) Sordahl (1990b)
	Rodent run	European Golden Plover, *Pluvialis apricaria* American Golden Plover, *Pluvialis dominica*	Williamson (1948) Byrkjedal (1989)
	Rapid run	Spotted Sandpiper, *Actitis macularius* Eurasian Oystercatcher, *Haematopus ostralegus*	Miller and Miller (1948) Williamson (1952)
	Wing-out run	Long-billed Curlew, *Numenius americanus*	Graul (1971)
Injury-feigning	**Broken-wing display**	Alpine Accentor, *Prunella collaris* Snowy Owl, *Bubo scandiacus* Florida Sandhill Crane, *Grus canadensis pratensis* Black-winged Stilt, *Himantopus himantopus* Piping Plover, *Charadrius melodus* Chestnut-belted Gnateater, *Conopophaga aurita* Red-crowned Crane, *Grus japonensis* Lesser Whistling-Duck, *Dendrocygna javanica* Kentish Plover, *Charadrius alexandrinus*	Barash (1975) Wiklund and Stigh (1983) Yosef (1994) Wijesinghe and Dayawansa (1998) Ristau (1993) Leite *et al.* (2012) Wang *et al.* (2013) Ranade and Prakash (2016) Gómez-Serrano (2018)

			Gómez-Serrano and López-López (2017)
	Erratic fluttering	Zenaida Dove, *Zenaida aurita* American Avocet, *Recurvirostra americana*, and Black-necked Stilt, *Himantopus mexicanus* Rufous Turtle Dove, *Streptopelia orientalis* Kentish Plover, *Charadrius alexandrinus*	Burger *et al.* (1989) Sordahl (1990b) Kameda (1994) Gómez-Serrano and López-López (2017)
	Exhausted bird	European Golden Plover, *Pluvialis apricaria* Eurasian Oystercatcher, *Haematopus ostralegus* Kentish Plover, *Charadrius alexandrinus*	Williamson (1948) Williamson (1952) Gómez-Serrano (2018) Gómez-Serrano and López-López (2017)
Displacement-type displays	**False brooding**	Arctic Skua, *Stercorarius parasiticus* Eurasian Oystercatcher, *Haematopus ostralegus* Western Sandpiper, *Calidris mauri* Killdeer, *Charadrius vociferus* Lapwings, *Vanellus* spp., Piping Plover, *Charadrius melodus* Kentish Plover, *Charadrius alexandrinus*	Williamson (1949) Williamson (1952) Brown (1962) Brunton (1990) Walters (1990) Ristau (1993) Gómez-Serrano (2018) Gómez-Serrano and López-López (2017)
	False feeding	Eurasian Oystercatcher, *Haematopus ostralegus* Black-winged Stilt, *Himantopus himantopus* Kentish Plover, *Charadrius alexandrinus*	Williamson (1952) Wijesinghe and Dayawansa (1998) Gómez-Serrano (2018) Gómez-Serrano and López-López (2017)
	Pseudo-sleeping	Eurasian Oystercatcher, *Haematopus ostralegus* Pied Avocet, *Recurvirostra avosetta*	Williamson (1950) Simmons and Crowe (1953)
	Nest betrayal	Common Ringed Plover, *Charadrius hiaticula*	Smith and Smith (1974)