

Nest predation research: recent findings and future perspectives

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Abstract Nest predation is a key source of selection for birds that has attracted increasing attention from ornithologists. The inclusion of new concepts applicable to nest predation that stem from social information, eavesdropping or physiology has expanded our knowledge considerably. Recent methodological advancements now allow focus on all three players within nest predation interactions: adults, offspring and predators. Indeed, the study of nest predation now forms a vital part of avian research in several fields, including animal behaviour, population ecology, evolution and conservation biology. However, within nest predation research there are important aspects that require further development, such as the comparison between ecological and evolutionary antipredator responses, and the role of anthropogenic change. We hope this review of recent findings and the presentation

of new research avenues will encourage researchers to study this important and interesting selective pressure, and ultimately will help us to better understand the biology of birds.

Keywords Animal behavior · Conservation biology · Evolution · Nest predation · Population ecology

Introduction

Predation is one of the most important selective pressures in nature, shaping evolutionary relationships in many systems including birds (Caro 2005). The life of all birds is characterized by a critical stage in which they are bound to a particular location, the nest. The selective pressures acting during this period modulate their biology to a large extent.

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Thus, it is not surprising that nest predation is considered a key source of selection for birds (Martin 1995).

Early arguments that nest predation can exert strong selection on species coexistence, habitat selection and life history strategies were met with skepticism (Ricklefs 2000). Avian ecology had focused on food limitation for a long period (Lack 1947; reviewed in Martin 1987, 1991), but a series of important papers championed the importance of predation (i.e. Moreau 1944; Skutch 1949; Martin 1988a, b, 1991, 1992, 1993a, b). Methodological improvements and new ecological perspectives have prompted many studies over the past 15 years, and these clearly demonstrate the importance of predation. For example, technology now allows researchers to monitor nests 24 h a day, which provides access to the identity and foraging behaviour of nest predators (e.g. Weidinger 2008; Benson et al. 2010). Advancements in our ability to measure physiological processes allow a better mechanistic understanding of the effects of nest predation risk, and the potential trade-off among different physiological systems within individuals (Zanette et al. 2014). Recent investigations on social information use by birds within communities have opened exciting new perspectives within this field (Dall et al. 2005; Seppänen et al. 2007; Schmidt et al. 2010). Furthermore, development of a more general predation framework has provided important new research challenges regarding nest predation, such as quantifying the magnitude of non-consumptive effects (the ecology of fear: Lima 1998; Cresswell 2008; Zanette et al. 2011). Indeed, the study of nest predation now forms a vital part of research in different areas, including animal behaviour, population ecology, evolution and conservation biology.

Our objectives are to highlight the relevance of nest predation within ornithology, discuss recent findings in the field, and address priorities for future research. Our aim is not to provide a comprehensive review; there are relatively recent reviews that cover different aspects of this field within the larger context of predation risk (Martin and Briskie 2009; Lima 2009; Magrath et al. 2010; Zanette et al. 2014). Rather, we provide insight into recent ideas and research that explore new aspects related to nest predation, or old aspects in light of recent conceptual advancements. We focus on studies directly addressing, or with clear implications to, nest predation, therefore not presenting those investigating predation in a broader sense.

Adult antipredator strategies

Pre-nesting antipredator strategies

Spatial and temporal variability in the risk of nest predation creates uncertainty for individuals about the quality of

breeding territories or nesting sites. An informed breeding site choice can increase the probability of reproductive success, making settlement decisions vitally important. Indeed, predator removal experiments show that birds respond to the presence of predators by altering settlement decisions (Fontaine and Martin 2006), and also alter settlement to experimental changes in habitat that alter predation risk (LaManna et al. 2015). How birds acquire information about nest predation risk before selecting nest sites is a topic of increasing research. In this section we explore the cues or information that individuals use to assess spatial and temporal heterogeneity in nest predation risk prior to settling for breeding and nest initiation. Understanding these cues provides insight into how nest predators can structure avian communities and demography.

Cues provided by nest predators

Indirect proximate cues of predator activity may be used by settling birds to avoid areas with nest predators. Avian prey respond to acoustic cues from predators (e.g. Zanette et al. 2011) and brood parasites (Forsman and Martin 2009), so that acoustic cues may provide reliable information about the presence of nest predators. For example, ground-nesting passerines eavesdrop on communication calls of Chipmunks (*Tamias striatus*), with lower nest densities found near playback sites (Emmering and Schmidt 2011). Acoustic cues of potential nest predators have also been shown to affect Siberian Jay (*Perisoreus infaustus*) and Orange-Crowned Warbler (*Vermivora celata*) decisions about nest location decisions (Eggers et al. 2006; Peluc et al. 2008). Natural environments can have several different predators, and birds appear able to incorporate acoustic cues of predators of both adults and nests during settlement (Hua et al. 2013).

Birds use olfactory cues and light reflected in the UV range in many activities, such as mate choice and foraging (reviewed in Hagelin and Jones 2007; Roth et al. 2008; Rajchard 2009; Caro and Balthazart 2010). Recent studies suggest that such cues may be important in settlement decisions too, particularly for detecting nest predator species that are non-vocal and nocturnal. At the territory scale, settling passerines and ducks avoided areas experimentally treated with nest predator urine and faeces, which simulated predator presence (Eichholz et al. 2012; Forsman et al. 2013). Similar cues may be used by ground-nesting Wood Warblers (*Phylloscopus sibilatrix*), which appear to avoid outbreaks of rodents that may in turn attract high densities of nest predators (Wesołowski et al. 2009; Szymkowiak and Kuczyński 2015). Indeed, several studies have used urine of potential nest predators sprayed onto nest boxes as a nest predator treatment, and have found responses consistent with a perceived increase in risk of

nest predation (Amo et al. 2008, 2011; Mönkkönen et al. 2009; Morosinotto et al. 2012). For example, nest boxes sprayed with mustelid urine are avoided (Mönkkönen et al. 2009). The mechanism used by birds to detect urine (odour, UV reflectance or both) is currently unknown. Research should focus on determining what cues are detected and used by settling birds to decrease probability of nest predation.

Protector species

Species vulnerable to nest predation may nest near aggressive species or predators that provide protection against nest predators (reviewed in Quinn and Ueta 2008). Protector species may serve as cues for low nest predation rates and may affect settlement decisions aimed at gaining safe nesting sites. Despite the generally clear reproductive benefits such associations entail (see Appendix 1 in Quinn and Ueta 2008), surprisingly few studies have experimentally demonstrated active choice in nest site selection in this context. Protective associations do not necessarily entail attraction at only small spatial scales; settling forest songbirds appear to preferentially select intermediate “optimal” distances from avian predator nests where the protective benefits against nest predators can represent a trade-off with the direct costs of being near the protector species (Thomson et al. 2006; Mönkkönen et al. 2007). Also bird species within the same guild may associate with each other during breeding to gain protective benefits (Kleindorfer et al. 2009; Campobello et al. 2012; Polak 2014); to date, these within-guild breeding associations have likely been overlooked, and deserve more attention in future. It would be fruitful to determine if prey actively choose to associate with other species for protection at different spatial scales, and the mechanisms involved in such associations, especially given the recent emphasis on positive interactions in avian communities.

The value of apparently protective associations may be dependent on the environmental context, and ‘protected’ nests may become prey when the abundance of alternative prey for the ‘protective’ predator declines (Dunn 1977; McKinnon et al. 2014). For example, fluctuating prey densities in different years appeared to alter the protection benefits to ground nests provided by Ural Owl (*Strix uralensis*; Häkkilä et al. 2012), which may also attract mesopredators seeking protection. This can in turn increase nest predation rates for ‘protected’ species (Morosinotto et al. 2012). Associations between species may also entail reciprocal protective relationships, for example the mixed breeding colonies of Lesser Kestrels (*Falco naumanni*) and Jackdaws (*Corvus monedula*) where both species decrease vigilance when in mixed colonies (Campobello et al. 2012). Overall, the use of protector species and their

impact on territory and nest site selection is probably underestimated, and might prove to be an important tool in species management (Fletcher 2008).

Assessing the success of others

Settling birds may use the presence or success of conspecifics and heterospecifics as proxies of nest predation risk. Assessing territories and nest sites both during (Parejo et al. 2008; Thomson et al. 2013) and following breeding attempts may affect breeding location decisions the following year (Boulinier and Danchin 1997; Doligez et al. 2002; Pärt et al. 2011). Prior to breeding, later arriving individuals can also assess the quality and success of earlier conspecific and heterospecific birds, and select nest sites that have features associated with success (Seppänen and Forsman 2007; Seppänen et al. 2010; Loukola et al. 2012).

Personal success as information

Birds can use personal reproductive performance as a guide to future habitat selection (e.g. Chalfoun and Martin 2010a; Pakanen et al. 2014). The “win–stay:lose–switch” strategy, proposed by Hildén (1965) and Greig-Smith (1982), suggests that individuals should return to a breeding site if successful, but leave if not. This hypothesis was originally tested in relation to patch-scale fidelity (e.g. Bollinger and Gavin 1989; Hoover 2003), a scale at which it might be an evolutionary stable strategy (Schmidt 2001). However, the win–stay:lose–switch rule is likely to operate at multiple scales, including within patches (Chalfoun and Martin 2010a; Kearns and Rodewald 2013), where individuals can reuse or change nest sites both between and within years.

The win–stay:lose–switch rule is also simplistic in some contexts because individuals are likely to benefit from taking a longer view of success than just the most recent breeding attempt. For instance, Piper (2011) has suggested the concept of site familiarity, in which individuals gain ‘private value’ based on their broader experience within a site. Similarly, individuals might follow a Bayesian updating rule that is cumulative over different nest attempts (Schmidt and Whelan 2010), which could be particularly important if individuals renest multiple times within a season (Pakanen et al. 2014). And as a Bayesian process, the posterior estimate of habitat quality accounts for the other information on distribution of quality among sites or habitats. These possibilities could be tested because, for instance, the Bayesian rule predicts birds will be less likely to alter habitat selection as a result of recent failure if they have a higher prior estimate of site quality, which could be manipulated experimentally.

Last, assessing conspecific success (see section “Assessing the success of others”) can be seen as the

extension of using personal success as information, and the two strategies may co-occur (Doligez et al. 2003) or the latter may supplement personal success, especially in colonial breeders (Boulinier and Danchin 1997).

Understanding individual habitat selection strategies, however, is not the same as understanding breeding habitat selection at the population level. As a result of frequency-dependent feedback from the action of other individuals a population may consist of individuals using different strategies. For example, those used by information producers or scroungers (Doligez et al. 2003), strategies which may be contingent on success or the fidelity of conspecifics (Pärt et al. 2011), and different strategies based on the effort (e.g. time) invested in collecting information which will depend on the intensity of competition for breeding sites (Schmidt et al. 2015).

One potentially fruitful approach to look beyond individual strategies is through the analogy of choosing a coloured ball (or balls at the population level) from an urn under the constraint that sampling is without replacement and (i.e. choice of breeding site) is biased. Information from pre- or post- and personal or conspecific breeding cues, or any inherent preference, is reduced to sampling bias (Schmidt et al. 2015). This approach is amenable to a game-theoretical analysis of breeding habitat selection that extends to investigating the ecological and evolutionary consequences of environmental change. For example, as population densities decline in degraded environments individuals are expected to invest more time in information gathering and exhibit greater bias toward selecting good sites. This suggests that information-gathering strategies have the capacity to ameliorate environmental change (Schmidt et al. 2015).

Antipredator strategies during the nesting stage

After settlement decisions are made, parents can adjust their breeding strategies in response to changes in nest predation risk (reviewed in Martin and Briskie 2009). Indeed, many of these proximate shifts in parental care behaviours have been the focus of recent studies, such as changes in incubation patterns (e.g. Chalfoun and Martin 2010b; Ibáñez-Álamo and Soler 2012; Morosinotto et al. 2013a) and offspring provisioning rates (e.g. Zanette et al. 2011; Ghalambor et al. 2013; Mutzel et al. 2013; Hua et al. 2014). The norm regarding these parental care traits is to reduce activity in response to increased predation risk, at least in ecological time. See below for the contrast between these responses and those obtained in evolutionary time.

Although the increased risk of predation has a predictable effect on incubation patterns and provisioning rates, it is less clear how risk affects egg mass and clutch size. There is a trade-off between egg size and number

(Smith and Fretwell 1974) and are both expected to decrease under increased nest predation risk (Martin et al. 2006; Martin and Briskie 2009). Despite this, recent studies on temperate passerine birds that experimentally manipulated predation risk found contrasting results. For example, Fontaine and Martin (2006) found that when predation risk was higher, females of eight species did not change clutch size but laid smaller eggs, which caused lower clutch masses. Conversely, other studies found a reduction in clutch size (Eggers et al. 2006; Travers et al. 2010; Zanette et al. 2011; Hua et al. 2014), and an increase in egg mass (Zanette et al. 2011) or no change in clutch mass (Hua et al. 2014) when predation risk was increased. The discrepancies among these results highlight the need for further tests. Changes in clutch size are potentially favoured over changes in egg mass since a decrease in clutch size represents a more significant decrease in energy investment—with fewer eggs to produce, incubate, and young to feed—than changes in egg mass (Martin et al. 2006). The dissimilar results found by Fontaine and Martin (2006), where birds adjusted egg mass but not clutch size, may be explained by a key methodological difference among experiments. Unlike the other four studies that increased risk, Fontaine and Martin (2006) decreased risk for eight species. Increases in clutch size with decreased risk represents a substantial increase in reproductive effort and, thus, may be constrained, whereas species may more readily decrease clutch size and associated reproductive effort when risk increases. Effects of opposing directions of risk on reproductive output have not been directly tested. Furthermore, species that already have very small clutch sizes, such as those in the tropics, may be constrained and less likely to further decrease clutch size in response to predation and may instead show changes in egg mass (Martin et al. 2006). These ideas require further testing to elucidate which factors may constrain or modulate parental responses in egg investment to changes in nest predation risk.

Offspring antipredator strategies

In contrast to their parents, who have active antipredator strategies, offspring are often seen as passive victims. Skutch beautifully captured this image of defenceless young when he wrote of naive nestlings begging when disturbed: “Doubtless they greet in this trustful manner the snake or squirrel that comes to devour them” (Skutch 1976). In this section we show that while young are certainly vulnerable, they are not helpless, but instead engage in a variety of behaviours to thwart predators. We focus particularly on the relatively recent issue of how young gain information about current risk from multiple sources,

including parents, predators and from other prey species. We suggest that research will benefit from taking a nestling's view of the world.

Antipredator behaviour

Young can thwart predators in a diversity of ways, including by reducing the risk of detection, recruiting parents, actively repelling predators, and fleeing (reviews: Skutch 1976; Martin 1992; Lima 2009; Magrath et al. 2010). Nestlings can reduce the risk of detection by crouching low in the nest and becoming silent if a predator is near, and begging calls themselves can be difficult for predators to overhear or locate, or young may beg silently (Wegrzyn and Leniowski 2015). Young can recruit parents through loud distress calls, which might also warn siblings. Distress calls could also repel predators, and some young appear to deter predators by mimicking dangerous species, such as Burrowing Owls (*Athene cunicularia*) producing sounds that resemble rattlesnakes (Rowe et al. 1986; Owings et al. 2002), and Northern Flickers (*Colaptes auratus*) sounding like a hive of bees (Wiebe and Moore 2008); however, these ideas remain to be tested (Dalziell et al. 2014). Nestlings can also use chemical defence (reviews: Dumbacher and Pruett-Jones 1996; Hagelin and Jones 2007). For example, Eurasian Hoopoe (*Upupa epops*) nestlings produce malodorous fluid from oil-glands and eject liquid faeces against potential nest predators (Glutz Von Blotzheim and Bauer 1980). The effectiveness of chemical defence has recently been experimentally tested for young Eurasian Rollers (*Coracias garrulus*), which vomit a cocktail of chemicals that deters dogs (Parejo et al. 2013), and for Great Spotted Cuckoos (*Clamator glandarius*), which defend themselves with a cloacal secretion containing a mixture of chemicals that deters both mammalian and avian predators (Canestrari et al. 2014). Finally, older nestlings commonly “explode” from the nest and seek cover if the nest is attacked.

Gathering information

When young have several options available, the choice of which defensive strategy to deploy may depend on the type of threat, opening up new opportunities for research on the perceptual and decision-making abilities of nestlings. Here we focus on information gained from sound, as this is valuable even before their eyes are open, as well as in enclosed nests or dense cover.

Information from parents

The most obvious source of information is from parents, whose alarm calls can warn young of danger (reviews:

Martin 1992; Caro 2005; Magrath et al. 2010). Nestlings commonly become silent after playback of parental alarm calls, showing that young respond to the signals themselves. Although responding to parental calls might seem a “passive” response compared to their parents’ “active” delivery of calls, communication requires the evolution of both signals and responses (Maynard Smith and Harper 2003), so the behaviour of young is best seen as active use of available information.

The active role of young in response to parental calls is best illustrated by differences in behaviour according to the type of danger or stage of development. Most dramatically, Great Tits (*Parus major*) respond differently depending on the type of parental alarm call, and therefore type of threat (Suzuki 2011). Young crouch at the bottom of their nest cavity when parents warn of crows, but flee the nest when parents give a different alarm call warning of snakes. These contrasting responses make sense because crows can reach into cavities but cannot enter nests, so crouching can avoid a probing beak, whereas snakes can enter nests and so young must flee. Similarly, White-Browed Scrubwren (*Sericornis frontalis*) nestlings become silent in response to parental mobbing calls warning of predators on the ground, but ignore aerial alarms to raptors flying overhead (Platzen and Magrath 2005). This difference is consistent with their vulnerabilities, because nests are cryptic, enclosed structures, placed on the ground and invisible from above. As soon as young leave the nest, however, they become highly responsive to aerial alarms (Magrath et al. 2006).

Information from predators

In addition to relying on calls from parents, young could gather information on risk from predators themselves. Adult vertebrates often recognize the vocalizations or other cues of predators (Hettner et al. 2014), but there is extremely little known about young. However, young birds can use acoustic cues from predators. Most White-Browed Scrubwren nestlings become immediately silent in response to playback of the sound of a predatory bird walking in leaf litter near the nest, which is similar to their response to parental alarm calls (Magrath et al. 2007). This response appears specific to the context of predation, since non-alarm vocalizations of parents and a variety of novel sounds prompt little or no call suppression in nestlings (Haff and Magrath 2010). This raises unanswered questions of generality and mechanism.

Information from other species

As well as listening to parents and detecting predators directly, young can gain information by eavesdropping on the alarm calls of other prey species, but it is not yet clear if

this is widespread. Eavesdropping on species with shared predators should be beneficial, and it could also be common, given that the adults of many species do eavesdrop on heterospecific alarm calls (reviews in Seppänen et al. 2007; Goodale et al. 2010; Magrath et al. 2014).

Among the few species studied, young nestlings usually respond only to conspecific alarm calls unless heterospecific alarm calls are very similar (e.g. Davies et al. 2004; Madden et al. 2005; Haff and Magrath 2012), but older nestlings may also respond to dissimilar heterospecific alarm calls. For example, White-Browed Scrubwren nestlings respond to the mobbing calls of conspecifics and one acoustically similar species when young, but respond to two other species with acoustically different calls later in the nestling period (Haff and Magrath 2012). There is a similar pattern among fledglings. Recently fledged young ignore heterospecific aerial alarm calls but do respond 2 weeks later, unless the heterospecific is rare on the territory (Haff and Magrath 2013). This suggests that young learn to recognize the alarm calls of common heterospecifics.

The predator point of view

In addition to adults and offspring, there is a third player in nest predation events: the nest predator. The predator perspective has been partially neglected in studies of predation risk (Schmidt 1999; Chalfoun et al. 2002a, b; Lima 2002). Within nest predation research, however, predators gain focus in part because cameras permit non-stop monitoring of bird nests. This allows for predator identification (Cox et al. 2012a), and an understanding of how predators find nests (Pelech et al. 2010). Nevertheless, there is minimal knowledge of many aspects of nest predator foraging habits, the mechanisms of locating nests, interactions between nest predators and habitats, and the importance of nest contents as food to individual predators (but see Schmidt et al. 2001; Schmidt and Schauer 2007).

Monitoring of bird nests has permitted individual predator species to be identified, and their prevalence and role in nest losses to be quantified (Cox et al. 2012a, b). Nest monitoring by cameras seems to be generally safe for nests (Weidinger 2008; Richardson et al. 2009; Ibáñez-Álamo et al. 2012), but validating this assumption in specific studies is important. Predator identification should be a critical starting point to studies investigating nest predation responses of a species or community to nest predation (e.g. Weidinger 2009). Knowing predator identity allows for better understanding of the selective pressures influencing parental and offspring antipredator strategies. Both cameras and dataloggers can provide insight into temporal patterns of predation, both within a day

(e.g. crepuscular, diurnal, nocturnal) and during the nesting cycle (Libsch et al. 2008; Biancucci and Martin 2008; Weidinger 2010). Predators may have different preferences or abilities to handle nest contents, such as in the case of highly specialized egg-eating snakes (e.g. Gartner and Greene 2008) or raptors that may prefer to eat nestlings over eggs (Cox et al. 2012b), which may in turn favour completely different antipredator adaptations. Indeed, non-specific nest predation data obscure potentially important aspects of the ecology of predators that limit understanding of avian responses to nest predators (Benson et al. 2010). Certainly some nest predation events are opportunistic (Schmidt 2004), but nest predators can use prior experience to learn nest site locations (Sonerud and Fjeld 1987; Pelech et al. 2010; Weidinger and Kočvara 2010).

Nest predators likely use a variety of predator-specific strategies and cues to find nests. Parental activity is one visual cue predators use to find nests. Several studies show that parents decrease activity under increased nest predation risk (see “[Ecological versus evolutionary strategies](#)”). The conspicuousness of the nests itself or the colours of the eggs may also attract the attention of visually oriented predators (Cott 1940; Tinbergen et al. 1962; Weidinger 2001; Kilner 2006; Biancucci and Martin 2010; Stoddard et al. 2011). Acoustic cues are generated around nests and are used by predators, and nesting birds respond by decreasing these cues in high risk situations (see “[Offspring antipredator strategies](#)”). Begging nestlings may attract predators (e.g. McDonald et al. 2009; Haff and Magrath 2011; Ibáñez-Álamo et al. 2012), and novel research suggests that nestlings of some species with high nest predation risk may beg silently (Węgrzyn and Leniowski 2015). Mobbing calls by parents at or near nests can also attract predators (Krama and Krams 2005; Krams et al. 2007; Bonnington et al. 2013), and indeed all acoustic communication by birds near the nest may be risky (Haff et al. 2015). Olfaction too has received recent attention. For example, alien predator Black Rats (*Rattus rattus*) can use odour to find bird nests, and this can be exploited as a management tool (Price and Banks 2012). Exposing rats to nest odours in an area prior to placing artificial nests caused non-associative learning that decreased subsequent nest predation rates. However, the presence of an obvious source of odour in nests, faecal sacs, did not seem to increase nest predation risk in blackbirds (Ibáñez-Álamo et al. 2013, 2014).

For birds nesting in environments with multiple nest predators, the challenge for parents and offspring is to limit the availability of cues used by predators. Understanding and quantifying the relative importance of these predation mechanisms will reveal how predation risk varies spatially and temporally, and improve our understanding of parental and offspring responses to changes in risk. In addition, nest

predators may actively hide inadvertent information of their presence (e.g. Loukola et al. 2014), and so open novel co-evolutionary pathways between birds and nest predators.

Physiological effects of nest predation

The physiological mechanisms by which predation could shape traits of animals have gained increasing attention in recent years, although they are still poorly understood (Sheriff and Thaler 2014). This is also true for nest predation, which constitutes only a small proportion of studies in birds (reviewed in Zanette et al. 2014), with most focus on behavioural or evolutionary changes instead (see above and below respectively). Nevertheless, the physiology of antipredator strategies is important because it allows the measurement of previously unconsidered costs, and may reveal interactions between nest predation and other selective pressures (e.g. Schwabl et al. 2007; Coslovsky and Richner 2011a).

Effects on adults

The most studied physiological effects of nest predation are on adult hormonal modifications. For example a comparative study including six North American passerines found that species with higher nest predation risk had higher baseline corticosterone levels, but this effect was not maintained at the intraspecific level as adults did not change their corticosterone levels when nest predators were removed from experimental areas (Fontaine et al. 2011). Similarly, other studies failed to find changes in hormone levels after experimental manipulation of nest predation risk (Silverin 1998; Butler et al. 2009). In contrast, Song Sparrow (*Melospiza melodia*) adults subjected to frequent nest predation or breeding in risky areas did increase their corticosterone levels (Clinchy et al. 2004, 2011; Travers et al. 2010). The results suggest that there is no general pattern in adult hormonal response to nest predation risk, probably due to the costs associated with some hormones (e.g. Kitaysky et al. 2003; Saino et al. 2003).

Antipredator behaviour could also place energetic demands on parents. Reduced food intake of “fearful” adults or lower male feeding of incubating females could affect their physiological state (Fontaine and Martin 2006; Zanette et al. 2013). Furthermore, changes in offspring development rates due to nest predation risk might reduce (i.e. fewer parental care behaviours) or increase adult energetic demands too (i.e. through maternal effects; see below), an interesting possibility that is worthy of further research.

Changes in the immune system or in oxidative stress might be other physiological costs of nest predation. In

fact, Song Sparrows when breeding in areas of high perceived nest predation risk showed an increase in basophils, but no elevation in heterophil to lymphocyte ratio suggesting that only some components of the immune system are affected by this selective pressure (Clinchy et al. 2004). Furthermore, frequent nest predation suppresses the immune system of female Song Sparrows, perhaps as a response to the threat of predation or the increased cost of egg production (Travers et al. 2010). These two studies also found increased oxidative stress in response to nest predation, which is consistent with the response to predation risk in general (reviewed in Constantini 2014). Nevertheless, more experimental studies across different species are needed to generalize about patterns of changes in the immune system or antioxidant protection. Comparative analyses will be especially valuable.

Effects on offspring

Direct effects of nest predation on offspring

The impact of nest predation risk on the endocrine system of nestlings seems to depend on the cues they perceive. Direct acoustic cues of nest predators decreased corticosterone but increased testosterone levels in the Common Blackbird (*Turdus merula*), suggesting that hormones might mediate begging activities according to perceived risk (Ibáñez-Álamo et al. 2011). However, conspecific alarm calls did not modify hormonal profiles in other species (Dufty and Crandall 2005; Rivers et al. 2011), and nestling distress calls produced elevated corticosterone levels only in older nestlings (Fridinger et al. 2007; Tilgar et al. 2010). This highlights the relevance of offspring age in the ability to respond, at least physiologically, to nest predation risk.

The immune system and risk of nest predation seem to be linked in nestlings. The cell-mediated immune response of Campo Flicker (*Colaptes campestris*) nestlings affects their ultimate antipredator strategy when captured by a potential predator: individuals with higher immune ability give louder distress calls, which could indicate a healthier status aimed at attracting potential adult defenders (Goedert et al. 2014). Part of the nestling immune system seems to be impaired by nest predation; the heterophil to lymphocyte ratio increased when chicks were exposed to conspecific nestling distress calls, suggesting that they were physiologically stressed (Tilgar et al. 2010). Nevertheless, it is still untested whether other less extreme manipulations could elicit changes in the immune response of offspring. For a broad understanding of these effects it is important to quantify not only single measures of the immune system but also different components simultaneously as recommended by experts in the field of ecoimmunology (e.g. Matson et al. 2006).

Nest predation effects on offspring mediated by adults

Risk posed by nest predators can affect offspring physiology indirectly through their effects on parents, such as through maternal effects (e.g. Martin and Schwabl 2008). Adult predation risk may affect the performance of offspring (e.g. Coslovsky et al. 2012), but only two studies have tested the effect of nest predation risk itself. For example, high levels of testosterone and 5α -dihydrotestosterone in eggs are positively correlated with nest predation risk in 25 songbirds (Schwabl et al. 2007). Moreover, Pied Flycatchers (*Ficedula hypoleuca*) laying eggs in sites with nest predator cues transferred more immunoglobulins to their eggs while lysozyme and carotenoid levels remained unchanged (Morosinotto et al. 2013b). These results suggest that mothers could be preparing offspring for an environment with a high risk of nest predation. However, a distinction between allocation (adaptive) and transfer (non-adaptive) is needed, as female flycatchers under adult predation risk also show higher immunoglobulin levels (Thomson et al. 2010), and therefore the adaptive significance of these changes in egg composition remains unknown.

In addition to maternal effects on egg composition, adults could affect the energetic demands of their offspring by means of changes in their incubation or brooding patterns (Martin et al. 2007; Martin and Schwabl 2008) or in their food delivery (see below). These parental effects, in turn, may interact with trade-offs in development of phenotypic traits to influence embryo and nestling development (e.g. Coslovsky and Richner 2011b; Cheng and Martin 2012; Martin 2014). Indeed, despite the strong relationship between development strategies and the risk of nest predation (von Haartman 1957; Remeš 2007; Martin et al. 2007, 2011) the underlying physiological mechanisms need further work. It is also important to consider differences between ecological and evolutionary responses, as the physiological traits that could be modified might differ.

Ecological versus evolutionary strategies: time scale matters

The influence of nest predation risk on the expression of life-history traits can reflect both proximate responses via phenotypic plasticity and evolved responses (reviewed in Martin and Briskie 2009). Proximate responses through phenotypic plasticity can allow fine-tuned responses to changing risk in ecological time. However, the extent of phenotypic adjustments can be constrained by trade-offs related to the evolved expression of traits, which differ among species (Martin and Briskie 2009). Moreover, the fitness consequences of shifts in a trait can differ

dramatically in ecological versus evolutionary time (Martin et al. 2015).

Phenotypic plasticity responses to nest predation risk of the same trait can clearly differ among species. For example, several songbird species responded to a taxidermy model of a nest predator by decreasing the rate at which they fed their young (Ghalambor et al. 2013). On its own, this result is not surprising since several experiments have demonstrated decreased provisioning with increases in nest predation risk (reviewed in Martin and Briskie 2009; see also: Zanette et al. 2011; Mutzel et al. 2013; Hua et al. 2014). However, species differed strongly in the degree of their plasticity responses to the perception of increased nest predation risk (Ghalambor et al. 2013). This variation in plasticity across species highlights issues for further work. First, plasticity itself (or reaction norms) can evolve differentially among species and may be related to intensity of nest predation risk (reviewed in Martin and Briskie 2009; Ghalambor et al. 2013). For example, species that use relatively safe cavity nests may exhibit less plasticity than species that use riskier open-cup nests. Second, the extent of plasticity may also differ because of constraints imposed by trade-offs with other traits. For example, provisioning plasticity in response to nest predation risk may be constrained by food needs of growing nestlings, and also modified by the number of nestlings and their evolved growth rates (Martin et al. 2011; Mutzel et al. 2013). Third, fitness costs of proximate changes in expression of traits can differ among species as a function of evolved physiological mechanisms (see below; Martin et al. 2011). Thus, differences among species in plasticity, and the costs and trade-offs, remain a relatively unexplored area in need of more research.

Fitness costs of changes in traits can differ strongly for proximate versus evolutionary responses, but these differences have not received sufficient attention. For example, increased nest predation risk can yield a decrease in provisioning rate in both ecological time through plasticity (reviewed in Martin and Briskie 2009; also Zanette et al. 2011; Mutzel et al. 2013; Hua et al. 2014), and in evolutionary time as seen among species (Martin et al. 2000, 2011). Reductions in provisioning in response to increased predation risk in ecological time can yield poorer quality and slower growth of nestlings (e.g. Zanette et al. 2011). Increased nest predation is expected to favour faster growth in evolutionary time (Lack 1948; Bosque and Bosque 1995; Martin 1995; Remeš and Martin 2002), and species with greater nest predation risk evolve faster growth and an associated reduction in provisioning rates (Martin et al. 2011). The reduction in food delivery in high risk species compared with low risk species does not carry the costs observed from reduced food delivery in ecological time. The costs of reduced food delivery in ecological time

within a species cannot be easily ameliorated because the developmental program (interaction and trade-offs among physiological and morphological traits) has evolved as an integrated whole. Over evolutionary time, however, trade-offs among physiological and morphological traits can shift to facilitate faster growth despite reduced food (Cheng and Martin 2012).

Another example of the differences in fitness costs of shifting traits in ecological versus evolutionary time is provided by further consideration of growth rate. Evolution of faster growth, as expected from increased nest predation risk, is thought to create physiological costs that lead to greater adult mortality and shorter life (McCay 1933; Rollo 2002; Metcalfe and Monaghan 2003). Tests within species have demonstrated shorter life with proximate increases in growth rates (e.g. Rollo 2002; Olsson and Shine 2002; Lee et al. 2013). Yet, comparisons across species showed no relationship between growth rate and adult mortality rates (Martin et al. 2015), potentially because changes in growth rate over evolutionary time can allow evolutionary shifts in other traits, such as the fatty acid composition of mitochondrial cell membranes, which can offset physiological costs of faster metabolism and growth (e.g. Hulbert et al. 2007). Such physiological systems are likely much less plastic in ecological time, and thereby create constraints that impose costs to shifts in growth rates in ecological time that are not observed in evolutionary time.

Of course, shifting traits even in evolutionary time can come with costs related to trade-offs among traits and, thereby, influence evolution of other traits. For example, bird species that evolved under greater risk of nest predation may shorten the time they stay in the nest, and young may leave the nest (fledge) at an earlier developmental state (von Haartman 1957; Martin 2014). While leaving the nest quickly might minimize nest predation risk, the reduced developmental state may also create costs to survival of young after they leave the nest, as well as parental effort in raising those young, all of which might influence evolution of clutch size (Martin 2014). These interactions among traits and their fitness costs can influence evolution of life-history strategies and constrain the extent of phenotypic plasticity in tests of responses to changing predation risk within species.

Finally, life-history trait responses to nest predation in both ecological and evolutionary time may be modulated by differences among species in adult mortality. Life-history theory suggests that life-history strategies should respond to age-specific mortality (e.g. Law 1979; Michod 1979; Charlesworth 1980; Martin 2002, 2004). In particular, parental effort is expected to increase with increasing adult mortality, but decrease with increasing offspring mortality (Law 1979; Michod 1979; Charlesworth 1980; Martin 2002, 2004). This interplay of adult

and offspring mortality on expression of life-history traits has received insufficient attention.

Human impacts and conservation issues of nest predation

Habitats worldwide continue to change rapidly, which can alter historic predator–prey relationships. Human-induced rapid environmental change can result in habitat loss, habitat fragmentation and/or alteration of remaining habitat patches, all of which can alter nest predation risk in comparison to contiguous patches of similar habitat devoid of human interference. Patterns of nest predation in relation to various forms of anthropogenic change, however, have been mixed. A huge body of literature, for example, has focused on nest survival in relation to different types of habitat edges, with varied and context-specific results (e.g. Lahti 2001; reviewed for tropical areas in Vetter et al. 2013). Urbanization and agricultural activities can influence nest predation, especially via the provision of food subsidies to predators. The directionality of such effects, however, depends on the main predators and whether subsidies translate into higher or lower nest predation pressure (Tomiałojć 1979; Chace and Walsh 2006; Benson et al. 2010; Ibáñez-Alámo and Soler 2010a; Rodewald et al. 2011). In some cases, management activities geared towards other species, such as ungulate feeding stations, can attract nest predators and inadvertently increase nest predation risk (Selva et al. 2014). Extraction of energy resources continues to be an expanding human land use, and has also yielded contrasting nest predation patterns. Nest predation rates of three sagebrush songbirds (Hethcoat and Chalfoun 2015) and the Greater Sage-Grouse (*Centrocercus urophasianus*; LeBeau et al. 2014) increased with natural gas and wind energy development, whereas other energy development studies suggest neutral (Hatchett et al. 2013) or even positive (Rubenstahl et al. 2012) relationships between energy development and nest predation. Recent ground-breaking work suggests that noise pollution is one of the factors by which energy development (and other human activities) can alter local trophic and predator–prey dynamics (Francis et al. 2009, 2011).

The presence of humans alone can have varying effects on nest predation rates. Adelie Penguin (*Pygoscelis adeliae*) hatching success and chick survival decreased with recreational visits by humans as a result of an increase of nest predation by skuas (Giese 1996). Nest predation has been invariant with respect to other indices of human presence and activity, however, such as proximity to recreational trails (e.g. Lindsay et al. 2008). Potential investigator effects on rates of nest predation have been a concern in nest survival studies, so that ambient nest

survival rates are documented accurately. Investigator effects, however, have been rare (Ibáñez-Alámo et al. 2012) and for some species, inversely related to nest predation (e.g. Ibáñez-Alámo and Soler 2010b).

The introduction of alien species is another human activity that typically increases nest predation. For example, the introduction of rats and other non-native mammals has been responsible for the extinction and endangerment of many birds through their nest predation activities, especially for burrow-nesting birds and those on islands (reviews: Steadman 2006; Jones et al. 2007). Feral cats are a particularly pervasive problem as predators of bird nests and adult birds (Nogales et al. 2013). Eradication of non-native predators is often extremely challenging, and the success of eradication programs can depend on other factors, such as whether all non-native predator species are simultaneously removed to eliminate compensatory nest mortality (Oppel et al. 2014).

To understand how anthropogenic change and human disturbance affect nest predation requires knowing the ecology of nest predators (Chalfoun et al. 2002a, b; Thompson and Burhans 2003; Weatherhead and Blouin-Demers 2004; Benson et al. 2010; DeGregorio et al. 2014a). A wide variety of species depredate bird nests (Ribic et al. 2012), with different relative importance of each nest predator for each bird species (Rodewald and Kearns 2011; Cox et al. 2012b; Hethcoat and Chalfoun 2015). In fact, even the relevance of a single nest predator can vary among habitats (Thompson and Burhans 2003; DeGregorio et al. 2014b). Moreover, different nest predator species respond uniquely to habitat change (Chalfoun et al. 2002a, b; Marzluff and Neatherlin 2006). A critical first step in mechanistic studies of nest predation in human-altered environments is therefore the identification of the major nest predator species, which while logistically challenging, pays large dividends in terms of understanding nest predation risk (Rodewald and Kearns 2011; Cox et al. 2012b, c; Ribic et al. 2012). Increased nest predation can result from multiple pathways, including increased predator abundance, activity and/or effectiveness. Simultaneous study of nest predation rates and nest predator abundance and/or behaviour across the same habitat gradients has therefore clarified mechanistic pathways of nest predation dynamics (Marzluff and Neatherlin 2006; Francis et al. 2009; Benson et al. 2010; Rodewald and Kearns 2011; Cox et al. 2012b, c; DeGregorio et al. 2014a, b). Further investigations of the prevalence and effectiveness of parental and offspring nest defence tactics to particular nest predators in altered environments (Ribic et al. 2012; Bonnington et al. 2013) would also lead to a more holistic understanding of the contexts under which anthropogenic change is likely to elevate or reduce nest predation risk.

Climate change will impose additional complexity in terms of clarifying the causes of nest predation. Where ectothermic predators such as snakes are important, warming temperatures may increase nest predation rates (Cox et al. 2013; DeGregorio et al. 2014b). Over the long term, however, the influence of climate change will likely affect nest predation rates synergistically with other environmental stressors, and will depend on shifts in the distribution and behaviour of co-occurring predators and prey. Many frontiers remain in terms of understanding how nest predation dynamics will be affected by human-induced rapid environmental change such as climate change. Such frontiers will likely only be successfully conquered via careful study of the interactions between predators, prey and habitats.

Biases that currently exist in nest predation research

Future research in nest predation should address remaining biases including methodological approaches, focal species and study regions. Utilization of artificial nests is still widespread among the scientific community (e.g. Vetter et al. 2013; Selva et al. 2014) even though artificial nests often produce unrealistic patterns of nest predation (e.g. Weidinger 2001; Zanette 2002; Moore and Robinson 2004). The use of artificial nests can provide complementary and useful information for addressing some questions (e.g. Villard and Pärt 2004; Price and Banks 2012) and does allow one to test interesting hypotheses once specific nest predators of interest have been identified. Reduction of the costs of using camera technology should offer opportunities to investigate nest predator communities as well as nest predation patterns using real (and active) nests rather than artificial nests.

Passerines seem to be the focus of a disproportionate amount of nest predation studies. There is a general lack of investigations in other groups of birds (i.e. charadriiforms), which could provide significant information in some topics like the effect of coloniality or antipredator strategies of non-altricial species. Two recent studies with non-passerines show that attention on other groups of birds may help advance our understanding of nest predation. For example, Eurasian Roller nestlings have shown active chemical defence against nest predators, something not previously confirmed for passerines (Parejo et al. 2013). Furthermore, a study with the Great Spotted Cuckoo found that the antipredator repellent secretion produced by chicks of this species can benefit parasitized host nestlings, changing a classic brood parasitic relationship into a mutualistic interaction (Canestrari et al. 2014).

As expected, a geographic bias also exists in nest predation research. Most studies focus on forested temperate regions, while tropical regions are underrepresented (Vetter et al. 2013). Increasingly some research groups are focusing work in tropical areas (e.g. Martin et al. 2000, 2015; Ghalambor and Martin 2001; Shaw and Cresswell 2014), but we urge scientists with access to these and other relatively unstudied areas (i.e. boreal regions or arid habitats) to initiate the collection of baseline nesting and nest predator data.

Conclusions and future directions

Here we present a brief overview of the most important remaining frontiers in nest predation research. From the adults' point of view, knowledge of the full suite of cues and the mechanisms involved in nest site selection is lacking, and may be instrumental to future conservation planning. Additionally, factors influencing variation in the degree or direction of parental care responses to changes in nest predation risk are not yet well understood. In particular, inconsistent results across studies investigating parental investment in egg size and number given changes in nest predation risk highlight the need for further testing. A comparative experimental approach may help elucidate what factors constrain or favour plasticity in these two traits across species.

An offspring perspective also offers opportunities for further research. Young take an active role in managing the risk of predation by gathering relevant information about risk from parents, predators and other species, and respond appropriately according to their capability, vulnerability and the type of threat. Future studies in nest predation will be especially valuable if they focus on the development and ecological significance of eavesdropping, and the importance of direct assessment of danger. Another promising line of inquiry regarding offspring is the effect of maternal effects on nestling responses, as a source of prenatal information about risk. Females exposed to predator cues before laying can have nestlings that differ in physiology or behaviour, which could be at least partly an adaptive response to risk.

In addition, the study of nest predation will be also greatly enhanced via additional study of predators. Important nest predator species must be identified and not just assumed. The mechanisms of nest site detection by predators, moreover, and potential strategies prey use to avoid eavesdropping seem to be particularly promising future lines of inquiry.

Furthermore, our understanding of nest predation effects on individual physiology is still in its infancy. A more complete comprehension of the mechanisms underlying

adaptive antipredator strategies will require integration of ecological and physiological approaches. In doing so, more species should be investigated, with a special emphasis on offspring physiological changes. It will be useful to also integrate new ways of exploring the impact of nest predation, for example through the use of neurobiology (Clinchy et al. 2013), other cues (i.e. visual) in experiments, or the inclusion of additional immunological indexes. But possibly the most crucial contribution will be to investigate whether physiological changes (for adults or young) are adaptive.

From a more general perspective, differences in antipredator responses between ecological and evolutionary time deserve more attention. Interspecific comparative studies in trait responses to nest predation will complement our general understanding of factors influencing phenotypic plasticity of prey. For example, a comparative approach can help uncover potential costs associated with changes in nest predation risk that may constrain the degree of the response. Additionally, costs associated with selection of one trait can cascade down to influence traits across different life stages (e.g. Martin 2014). A focus on the demographic consequences of nest predation risk interacting with other important population level processes will also be important (e.g. Zanette et al. 2011; Sofaer et al. 2014), as they are crucial to detect the adaptive value of antipredator responses.

Finally, from a conservation standpoint, improved understanding of the mechanisms underlying variation in nest predation risk will be particularly critical in areas with human-induced habitat change. Such understanding will benefit from concomitant study of important nest predators and prey, across relevant habitat gradients and spatial scales. Other challenges regarding nest predation research that still remain are the study of other bird groups beyond passerines or other geographical areas different from the most commonly studied forested temperate regions. We hope that the forthcoming years will be fruitful in expanding our knowledge about this crucial selective force for birds.

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