

Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation

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ABSTRACT

A growing body of work suggests that breeding birds have a significant capacity to assess and respond, over ecological time, to changes in the risk of predation to both themselves and their eggs or nestlings. This review investigates the nature of this flexibility in the face of predation from both behavioural and reproductive perspectives, and also explores several directions for future research.

Most available work addresses different aspects of nest predation. A substantial change in breeding location is perhaps the best documented response to nest predation, but such changes are not always observed and not necessarily the best strategy. Changes in nesting microhabitat (to more concealed locations) following predation are known to occur. Surprisingly little work addresses the proactive avoidance of areas with many nest predators, but such avoidance is probably widespread. Individual birds could conceivably adopt anti-predator strategies based on the nest predators actually present in an area, but such effects have yet to be demonstrated. In fact, the ways in which birds assess the risk of nest predation is unclear. Nest defence in birds has historically received much attention, but little is known about how it interacts with other aspects of decision-making by parents.

Other studies concentrate on predation risk to adults. Some findings suggest that risk to adults themselves influences territory location, especially relative to raptor nests. An almost completely unexplored area concerns the sorts of social protection from predators that might exist during the breeding season. Flocking typical of the non-breeding season appears unusual while breeding, but a mated pair may sometimes act as a “flock of two”. Opportunistic heterospecific sociality may exist, with heterospecific protector species associations more prevalent than currently appreciated. The dynamics of singing during the breeding season may also respond to variation in predation risk, but empirical research on this subject is limited. Furthermore, a few theoretical and empirical studies suggest that changes in predation risk also influence the behaviour of lekking males.

The major influence of predators on avian life histories is undoubtedly expressed at a broad phylogenetic scale, but several studies hint at much flexibility on an ecological time scale. Some species may forgo breeding completely if the risk of nest predation is too high, and a few studies document smaller clutch sizes in response to an increase in nest predation. Recent evidence suggests that a female may produce smaller eggs rather than smaller clutches following an increase in nest predation risk. Such an increase may also influence decisions about intraspecific brood parasitism. There are no clear examples of changes in clutch/egg size with changes in risk experienced by adults, but parental responses to predators have clear consequences for offspring fitness. Changes in risk to adults may also influence body mass changes across the breeding season, although research here is sparse. The topics highlighted herein are all in need more empirical attention, and more experimental field work whenever feasible.

Key words: predation risk, anti-predator behaviour, nest predation, habitat selection, nest site selection, breeding season sociality, life-history flexibility, singing, lekking, body mass regulation.

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I. INTRODUCTION

The biology of breeding birds is among the most studied topics in the fields of evolutionary ecology and evolutionary biology. This fact reflects the long tradition of comparative work on the life-history characteristics of birds, especially as they relate to reproduction (e.g., Lack, 1947, 1968; Skutch, 1949; Ricklefs, 1969; see also Grant, 1986; Birkhead & Møller, 1992; Martin, 1995, 2004; Hansell, 2000). This work has not only illuminated the biology of birds, but influenced a great deal of early and current thinking in the study of evolutionary ecology (Martin, 2004).

This comparative emphasis in the study of breeding birds is certainly well placed, as much behavioural and life-history

variation in birds is expressed among species and at broader taxonomic/phylogenetic levels (e.g. Bennett & Owens, 2002). This is certainly the case for many key life-history traits such as body size, survivorship, clutch size, breeding/mating systems, developmental mode, *etc.*, all of which are relatively fixed within a given species compared to the broad sweep of variation found across the avian world (see also Martin, 2004). This too is true of variation in avian responses to predation, with adaptive responses in nesting biology, clutch size, sociality, feeding behaviour, *etc.*, most evident across species and broader taxonomic units (e.g. Ricklefs, 1969; Martin, 1995; Hansell, 2000). This latter work suggests that predation, specifically nest predation, is a clear and important driving force in the evolution of avian breeding biology.

A growing body of work suggests that the risk of predation also may influence many aspects of behavioural and reproductive decision-making in ecological time – that is, within the lifetime of individual breeding birds. My goal here is to gather and review this complementary “ecological time” literature and in doing so provide some new perspectives on avian breeding biology. More specifically, this review focuses on the way in which breeding birds manage the risk of predation (to themselves or to their offspring) within their lifetimes (as per Lima & Dill, 1990; Sih, 1994; Ydenberg 1994; Caro, 2005). Predation can vary greatly within a bird’s lifetime, and flexibility in response will undoubtedly lead to fitness benefits above those of fixed traits alone. I will explore the information available to breeding birds about predation risk, and the sorts of behavioural and life-history options that may allow them to manage that risk to themselves and to their offspring. These issues of information and options in the face of changing risk, and tradeoffs involved in making decisions (broadly defined), are constant themes throughout this review. Although beyond the scope of the present review, another of my goals is to help forge a link between flexible reproductive decision-making and studies of avian population and community ecology (e.g. Schmidt, 2006; see also Cresswell, 2008), much as studies of anti-predator decision-making have provided insight into population and community ecology in general (Lima, 1998; Preisser, Bolnick & Benard, 2005; Schmitz, 2008).

II. DEALING WITH NEST PREDATION

Nest predation is the most important source of reproductive failure for the great majority of birds (Ricklefs, 1969; Martin, 1993, 1995; Thompson, 2007). It is therefore useful to consider the many ways in which breeding birds might manage the risk of nest predation in ecological time.

(1) A change in nest location following nest predation

Nest predation is often so high that most birds require several breeding attempts to successfully rear young (Ricklefs, 1969). This is especially true of non-cavity nesting passerines, which often re-nest multiple times during a breeding season (Grzybowski & Pease, 2005). Multiple breeding attempts, both within and between seasons, can thus be viewed a common strategy of dealing with nest predation (Jackson, Rohwer & Nolan, *et al.*, 1989; Martin, 1992a; see below). Several options are available: to re-nest in the same site, in a different site within the same territory, or to engage in breeding dispersal (Harvey, Greenwood & Perrins, 1979; Greenwood & Harvey, 1982) to an entirely different territory/area for the next attempt or breeding season. Renesting at all of these scales has been examined, with most work focusing on breeding dispersal.

(a) Breeding dispersal

It is clearly beneficial to move to a different area following nest predation. Predators are potentially able to remember

the sites of nests (particularly permanent sites like tree holes), and may return in the future. Furthermore, long-lived predators may occupy a given range for several years. Theoretical models support such benefits of breeding dispersal (Switzer, 1997), and the simulation model of Powell & Frasch (2000) stresses that dispersal distance should depend on the home range of the predator involved. This simulation model does not (directly) assume that the predator has a memory for specific locations; including such an effect would strengthen its overall conclusion. Few studies demonstrate that nest predators re-visit depredated nest sites, although it is clearly a reasonable assumption.

Several cases of breeding dispersal are linked directly to nest failure during the previous nesting attempt(s). In an influential paper, Dow & Fredga (1983) found that female goldeneyes (*Bucephala clangula*) who suffered nest predation moved to new nesting cavities during the subsequent breeding season at twice the rate observed for successful nesters. This effect was attributed to predation by pine martens (*Martes martes*), whose presence suggests a long-term elevation of predation risk in a given area (see also below). Sonerud (1985) investigated pine marten predation on the eggs and offspring of Tengmalm’s owls (*Aegolius funereus*), and showed that recent predation was predictive of subsequent predation. He argued that this was why these owls preferred new nest sites to older ones (see also Sonerud, 1989). By contrast, Korpimäki (1987, 1993) worked in a location where these owls experienced lower nest predation but still showed much breeding dispersal, and argued that breeding dispersal in Tengmalm’s owl was driven mainly by local food depletion rather than predation. However, subsequent work at Korpimäki’s site indicated a major role for predation in owl breeding dispersal (Hakkarainen *et al.*, 2001; see also below).

A similar pattern has been shown for other species. Following nest predation within a given breeding season, stonechats (*Saxicola torquata*) moved farther than did successful pairs and changed nest cover type during the next nesting attempt (Greig-Smith, 1982). These stonechats also moved farther following the successful fledging of a large number of offspring; Greig-Smith (1982) considered this to be a possible anti-predator adaptation, but it might also reflect local food depletion. Orange-breasted sunbirds (*Anthobaphes violacea*) also move farther to new nesting sites following predation in a given season (Grégoire & Cherry, 2007), but showed no tendency to change cover type. Other studies show predation-related breeding dispersal. For instance, bobolinks (*Dolichonyx oryzivorus*) that experience reproductive failure (nest loss) tend to move to a new breeding site during the next year (Gavin & Bollinger, 1988). Doligez *et al.* (1999) found that collared flycatchers (*Ficedula albicollis*) show greater dispersal from habitat patches with lower reproduction (essentially greater nest predation) than from more productive patches. Similarly, Danchin, Boulinier & Massot (1998) showed that kittiwakes (*Rissa tridactyla*) often abandon a given nesting cliff after nest predation but tend to return the next year if breeding was successful. Such decisions may also be influenced by the breeding success of others in the local population (see below).

These ideas about breeding dispersal are amenable to experimentation, which can eliminate some of the uncertainty surrounding observational studies. For instance, a single staged encounter with a marten-like predator (an American mink, *Neovison vison*) induced long-range breeding dispersal in Tengmalm's owls (Fig. 1), even though the staged encounters did not lead to the loss of eggs or young (Hakkarainen *et al.*, 2001). Hoover (2003) showed that experimentally simulated nest predation or nesting success (replacement of depredated offspring) had a strong effect on the tendency of prothonotary warblers (*Protonotaria citrea*) to return to the same site during the following breeding season (Fig. 2). Similarly, American robins (*Turdus migratorius*) and brown thrashers (*Toxostoma rufum*) experiencing simulated nest predation moved to new breeding territories at twice the rate of successful birds (Haas, 1998). Finally, an experiment by Martin, Scott & Menge (2000b) provide rare evidence showing that predators are likely to return to previous sites of predation (see also Pöysä, 2006). By placing finch eggs in recently used nests of forest-nesting species, Martin *et al.* (2000b) showed that previous predation of a given nest closely predicted its future fate. Similar results were reported in an experiment with grassland-nesting birds (Muchai & du Plessis, 2005), but Cresswell (1997) found no such correspondence of nesting outcomes.

Moving to a new site may not always be the best option following nest predation. There are undoubtedly costs associated with such dispersal, and there may be relatively few options for new breeding areas. One could also imagine predatory environments in which prior predation does not indicate a higher future risk (e.g., Roth & Lima, 2007), although relevant information about predators is usually lacking (see Lima, 2002). A recent experimental study on northern flickers (*Colaptes auratus*) (Fisher & Wiebe, 2006) found no change in nesting site following either an experimental predatory encounter (with a squirrel), or actual nest predation. Perhaps such cases are more likely

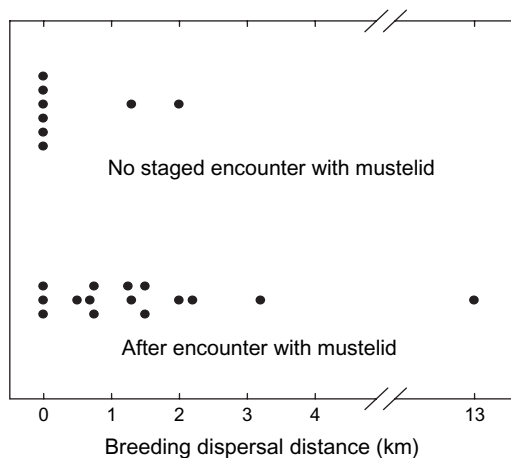


Fig. 1. Breeding dispersal by Tengmalm's owls (*Aegolius funereus*) in Finland that were or were not exposed to a staged encounter with a mustelid nest predator (a caged mink placed on the nest box). Owls exposed to the mustelid dispersed significantly farther than those not exposed (Mann-Whitney $U = 29.0$, $P < 0.05$); most of the latter did not disperse to new territories. Modified from Hakkarainen *et al.* (2001).

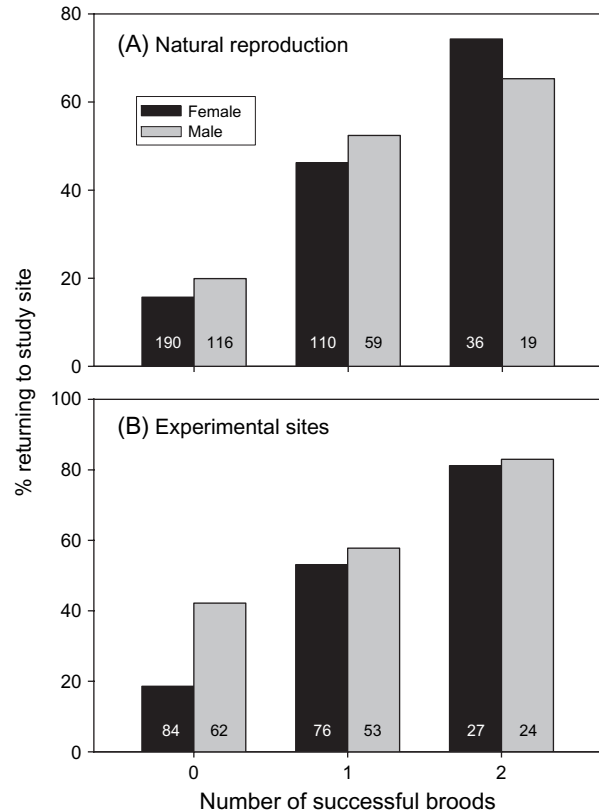


Fig. 2. Tendency of prothonotary warblers (*Protonotaria citrea*) to return to a given study site (bottomland forest fragments in Illinois, USA) as a function of (A) natural variation in the number of broods fledged successfully and (B) experimentally manipulated fledging success. The tendency to return to a given site increased significantly with breeding success in both groups (see Hoover, 2003). The very similar patterns in (A) and (B) indicate that the overall natural return tendency is related to nest success *per se* and not to other aspects of territory or bird quality. Numbers within bars represent the number of individual birds in the analyses. Modified from Hoover (2003).

when dealing with cavity nesting species, where nest site limitation is more likely than in other species.

A given bird may also decide not to move because it is already in the best nesting habitat. Hoover (2003) found such an effect in his experimental manipulation of breeding success in prothonotary warblers; a warbler experiencing nest failure tended to remain on its territory if its neighbours did not suffer nest predation. A similar effect was also apparent in kittiwakes (Danchin *et al.*, 1998; Boulinier *et al.*, 2008); birds nesting on the highest quality (low predation) cliffs were unlikely to abandon their nests sites following nest predation, whereas those on low-quality cliffs did so more readily. Such behaviour implies that birds can determine whether they are in the best nesting habitats. Such knowledge may be genetically programmed (Morse, 1980) or can be obtained by observing the nesting success of others (see Danchin *et al.*, 1998; Doligez *et al.*, 1999; Parejo *et al.*, 2007). Doligez, Pärt & Danchin (2004) suggest that collared flycatchers engage in prospecting trips designed to gain such information.

An intriguing aspect of predator-induced breeding dispersal is that its benefits should be predator-specific. Some predator species may typically be local or patchy in distribution and thus can be avoided, whereas others may have very large home ranges or may be so uniformly distributed that avoidance is not practical (Jackson *et al.*, 1989; Powell & Fransch, 2000). Predator-specific breeding dispersal requires that birds can identify the source of nest failure and act accordingly. This is clearly possible if a predator is observed in the act. However, it is not clear whether birds can otherwise discern the predator involved in nest destruction. There is apparently no direct information available on this topic, but results in Jackson *et al.* (1989) suggest that breeding dispersal in prairie warblers (*Dendroica discolor*) may indeed depend on the predation source.

(b) Smaller scale movement

For birds that do not disperse to a new area following nest predation, there may still be some benefit to nesting in another location within a territory or home range. For instance, following nest predation on relatively exposed nests, pinyon jays (*Gymnorhinus cyanocephalus*) build their next nest in a site farther below the canopy than do previously successful birds (Marzluff, 1988). Such lower sites are apparently safer, but offer a less favorable microclimate. Interestingly, there was a suggestion that pinyon jays nest lower each season as nest losses accumulate. Spotted antbirds (*Hylophylax naevioides*), which also occupy long-term territories, show a strong tendency to reuse a successful nest site (Styrsky, 2005); previously depredated sites were used again in future attempts, but not immediately following the failed attempt. On the other hand, Wiebe & Martin (1998) found little evidence that previous predation events altered the type of nest site chosen by white-tailed ptarmigan (*Lagopus leucurus*) in subsequent nesting attempts. Overall, it is likely that small-scale nest site relocations in response to predation are commonplace, but such decisions have received relatively little attention.

(2) Nest site location and the proactive avoidance of nest predation

The prevalence of nest predation suggests that selection would favour mechanisms allowing a bird to assess the risk of nest predation and to respond proactively. This sort of avoidance clearly occurs in adult birds when responding to risk to themselves (Lima, 1998; Caro, 2005; Cresswell, 2008). In a sense, breeding dispersal can be seen as a proactive effort to avoid future predation based on direct experience. However, studies taking an explicitly “proactive” perspective on nest predation are surprisingly few in number, particularly experimental studies.

(a) Small- to large-scale matters

A few recent experimental studies provide good examples of proactive responses to nest predators at smaller scales. Forstmeier & Weiss (2004) showed that the placement of nests within territories by dusky warblers (*Phylloscopus fuscatus*) varies

with the local abundance of small mammalian predators. In years with many chipmunks (*Tamias sibiricus*), nests were placed in safer sites farther from the ground and in more isolated bushes; the safety of such sites was established using artificial nests. The apparent cost of these safer sites is higher exposure to wind and possibly to parasitic cuckoos, and a higher foraging cost may be associated with isolated bushes. Employing an experimental approach, Eggers *et al.* (2006) used taped corvid calls to elevate the risk of nest predation perceived by Siberian jays (*Perisoreus infaustus*). The jays responded with a clear shift to safer but cooler nesting sites. Orange-crowned warblers (*Vermivora celata*) respond to novel nest predator playbacks by moving to ground nesting from sites in low trees and shrubs (Peluc *et al.*, 2008).

Observational studies on smaller scale nesting decisions are also uncommon. However, taking such an approach, Schmidt, Ostfeld & Smyth (2006) recently showed that veeries (*Catharus fuscescens*) place their nests in areas with low mouse activity, as verified by trapping. White-footed mice (*Peromyscus leucopus*) are serious but largely incidental nest predators (Schmidt *et al.*, 2001), and patchiness in their small-scale distribution allows effective avoidance. Similarly, Inca terns (*Larosterna inca*) show a clear preference for sites with the lowest nest predation, i.e. inaccessible crevices and close to a cliff’s edge (the latter being more related to adult safety; Velando & Márquez, 2002). Some tree species are also difficult for terrestrial predators to climb (Richardson & Vander Wall, 2007), but whether this influences nest tree selection by birds is unclear. Møller (1988) found that European blackbirds (*Turdus merula*) generally nested in the safest sites (as determined using artificial nests), but he found no apparent differences in site use related to the presence of nest predators (magpies, *Pica pica*); this result could indicate an absence of conflict between nest safety and other factors such as thermoecological constraints, but this was not examined. Common goldeneyes intent on parasitizing conspecific females show a preference for nests (tree cavities) that were successful in the previous year (Pöysä, 1999) or areas in which predation is low (Pöysä, 2003). Such information about the success of others was probably obtained *via* prospecting trips (Doligez *et al.*, 2004) made by females during the previous season. Such prospecting is strongly suggested by experimental work demonstrating that goldeneye females cannot assess the risk of nest predation in nest sites that have not yet been occupied (Pöysä *et al.*, 2001), and the fact that females preferentially parasitize nests in known successful locations (Pöysä, 2006).

So far, available studies suggest that at least some species can make predation-related adjustments to nest site selection within their normal nesting pattern. However, it appears that most birds do not switch to radically different sorts of nesting sites in response to changes in the risk of nest predation, say from ground nesting to tree-cavity nesting in the face of a large increase in ground predators. Experimental work by Fontaine *et al.* (2007) showing persistent and substantial differences in predation rate among various nesting locations (ground, shrub, and tree) suggests that a radical switch in nest site might well be advantageous (see also Yeh, Hauber & Price., 2007), but most species appear to be relatively inflexible regarding

basic nesting mode (see also Martin, 1993, 2001). A rare counterexample is the switch to ground nesting from shrubs and short trees by orange-crowned warblers following the simulated appearance of scrub jays (*Aphelocoma californica*) (Peluc *et al.*, 2008). Intriguingly, scrub jays do not normally occur on the islands that the warblers inhabit.

Fontaine & Martin (2006a) provide a rare and insightful model for experimental work at a relatively large spatial scale, which involved the removal of corvid and mammalian (squirrels) nest predators from small stream-drainage forests in northern Arizona. The reduction in nest predators led to higher densities of several migratory breeding bird species but not of permanent residents. It was not clear which of the classes of predator, avian or mammalian, was the more important for a given species. The information used by birds to assess the absence of predators was also not known, but the lack of predator vocalizations was probably involved (see also Eggers, Griesser & Ekman, 2005; Eggers *et al.*, 2006; Peluc *et al.*, 2008). In a quasi-experiment making use of a gull-control program on a British island, Finney *et al.* (2003) found that Atlantic puffins (*Fratercula arctica*) avoided higher densities of nesting gulls when establishing new burrows (see also Harris, 1980). These gulls are nest predators and also kleptoparasites of adults. Interestingly, puffins may use gulls as protectors from larger predators in other parts of the Atlantic (Pierotti, 1983).

A few observational studies suggest similar effects of variation in nest predator numbers at a larger spatial scale. In some areas of western Pennsylvania, ovenbirds (*Seiurus aurocapilla*) breed in atypical forest edge habitat that appears to lack chipmunks due to wet soil conditions (Morton, 2005). Red-backed shrikes (*Lanius collurio*) avoid occupying potential territories that are close to or within the territories of magpies (a nest predator); patterns of occupancy changed as the distribution of magpies changed over time (Roos & Pärt, 2004). Similarly, Tryjanowski, Goldyn, & Surmacki, (2002) found lower densities of ground-nesting birds within 500 m of red fox (*Vulpes vulpes*) dens in an agricultural landscape.

The spatial avoidance of nest predation can be apparent even at a scale of 100 km² or more, although few studies are at this scale. Lloyd *et al.* (2005) suggested that ovenbirds avoid entire landscapes that have high levels of predation and brood parasitism. A landscape-level analysis of nest site choice in common goldeneyes indicated broad patterns (many km²) of spatial avoidance that correspond to areas of high nest predation (Paasivaara & Pöysä, 2008). The preferred low-predation areas were, however, not necessarily those with the best food conditions for ducklings, and the distribution of breeding females post-hatching was not related to patterns of nest predation. This illustrates that nesting and brood-rearing sites may be spatially uncoupled in species with precocial young, unlike in altricial species.

Not all observational work is so clear-cut. For instance, Møller (1988) found that European blackbirds avoided nesting in smaller forest patches where magpie predation is higher, but did not avoid larger patches occupied by magpies. The magpies nested earlier than the blackbirds, hence such avoidance should have been possible. An apparent lack of ability to assess large-scale patterns in nest predation was found in the sage sparrow (*Amphispiza belli*) in southern

California (Misenhelter & Rotenberry, 2000). These sparrows show a preference for remnant native habitat over disturbed areas, but such preferred areas have higher nest predation from snakes (which perhaps found refuge in those remnant patches). Such native habitat might now function as a trap for sage sparrows (Misenhelter & Rotenberry, 2000). A multi-scale, community-level study of nest predator and songbird co-occurrence (Marzluff *et al.*, 2007) suggested that some (but not most) songbird species are negatively associated with nest predators; a complication here is that not all songbird species may be able to achieve such a negative association when faced with mobile nest predators, even if they attempt to avoid them (Sih, 1998). Similarly, although ovenbirds showed landscape-level avoidance of high nest predation, wood thrushes (*Hylocichla mustelina*) did not (Lloyd *et al.*, 2005). Finally, a multi-scale analysis of habitat selection by breeding Brewer's sparrows (*Spizella breweri*) found an influence of nest predation on smaller scale decisions, such as nest and territory placement, but no clear effect at larger spatial scales (Chalfoun & Martin, 2007).

(b) Protector species and the choice of nesting sites

A protector species (Haemig, 2001; Caro, 2005) is one whose aggressive nest defence is used by other species to defend their nests as well. Caro (2005) provides a broad discussion of protector species; their relevance here is restricted to nest placement. Clearly, nest placement by protectors will dictate the best nest sites for the protected species. This is particularly so when the association is largely obligate for the species seeking protection (e.g. Groom, 1992; Quinn *et al.*, 2003), but also applies when the association is more facultative (e.g., Bogliani, Sergio & Tavecchia, 1999).

Because most protector species are potentially dangerous to offspring and adults of the protected species (Caro, 2005), there is likely to be an optimal nesting distance between them. For example, nest predation suffered by red-breasted geese (*Branta ruficollis*) increases with distance from peregrine falcon (*Falco peregrinus*) nests, but these geese are also attacked or harassed if they nest too close to the falcons (Quinn & Kokorev, 2002). Most geese nested at least 40–50 m away, and some evidence suggests a tendency for the geese to nest farther from falcons in years with few nest predators. Mönkkönen *et al.* (2007) suggest a similar arrangement around goshawk (*Accipiter gentilis*) nests for some forest-dwelling bird species. Predation on artificial nests decreases as they are placed closer to goshawk nests, and accordingly, some small breeding birds that are not preyed-upon by the hawks nest in spatial association with them. Bird species appearing in the diet of goshawks showed a tendency to nest at intermediate distances from hawk nests. It is likely that further work on these flexible “protector arrangements” will show them to be fairly common in the avian world.

(3) Density-dependent predation and the spacing of nests

Do birds assess the local risk of predation and space their nests relative to each other such that this risk is lowered?

While this is virtually unstudied, there is enough work on density-dependent nest predation to suggest that such investigations of nest placement flexibility are worth pursuing.

A key point here is the degree to which nest predation is density-dependent. Caro's (2005) review of this topic yields a mixed picture. Most studies indicate density dependence, but in a significant minority, there was no such effect. This variability undoubtedly reflects differences in predator type and behaviour across study sites. Schmidt & Whelan (1999) argue that highly mobile predators with large home ranges and the necessary cognitive abilities (like raccoons and corvids) are more likely to drive density dependence than are more spatially restricted predators such as small rodents and some snakes. Few researchers have taken the idea of density-dependent nest predation further than Martin (1988, 1993, 1996), whose work suggests that nest predation is lower when local communities of breeding birds utilize diverse nest locations (in three dimensions), presumably challenging predator search tactics more effectively than would a higher density of similar nests in a given locale (but see Rangen, Clark & Hobson, 2001). It is reasonable to expect then that the presence of "density-dependent" predators will drive increased spacing of nests, especially with respect to those of conspecifics and other species with similar nesting requirements (see also Martin & Martin, 2001). One might also expect that birds would choose to nest in more diverse local communities when faced with certain types of nest predators (see also Martin, 1988). Of course, the spacing of nests (or territories) also may be influenced by a host of other factors, including the local density of conspecifics (e.g. Smith *et al.*, 2006), anti-predator benefits gained by having near neighbours (see below), the need to keep sexual competitors at a distance (Møller, 1990a), and the possibility that some local aggregations of territories may function as hidden leks (Fletcher & Miller, 2006).

All of these possibilities remain virtually unstudied, although Hogstad (1995) provides an exception in a study on fieldfares (*Turdus pilaris*). This thrush is unusual in its tendency to nest in colonies as a defence against nest predators (Wiklund & Andersson, 1980). These colonies are effective defences against avian predators such as corvids rather than large mammalian predators such as mustelids. Hogstad (1995) reasoned that mustelid predation on fieldfare nests would be more intense during years with few rodents (favoured mustelid prey), especially so if the birds remained in dense nesting colonies. His results show a clear tendency for colonies to form during years of high rodent abundance, and for nesting to be more dispersed (non-colonial) during low rodent years (Fig. 3). Hogstad (1995) suggested that fieldfares track rodent density directly as a surrogate cue of predation risk, but the exact cues used are unknown.

(4) Nest concealment

Greater nest concealment should lead to a lower probability of nest discovery by vision-based predators. One might thus expect birds to prefer maximally concealed sites. However,

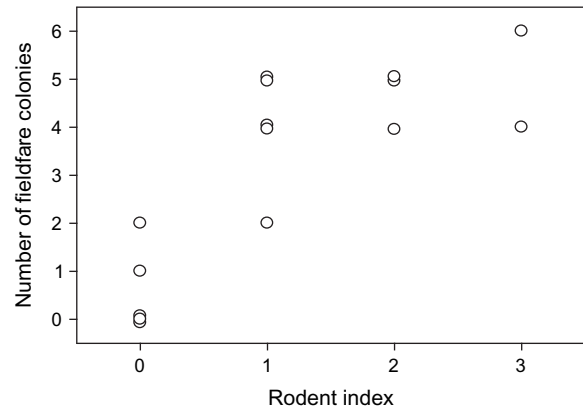


Fig. 3. Relationship between the number of fieldfare (*Turdus pilaris*) colonies and rodent density (an index derived from rodent tracks and sightings) at a site in Norway. Each point represents a single breeding season. Fieldfares were more likely to nest colonially as local rodent density increased (Spearman rank correlation, $r_s = 0.80$, $P < 0.001$). From data in Hogstad (1995).

many breeding birds face a more complex situation, and should benefit from an ability to assess and respond to the predatory environment in ecological time. For example, well-concealed nests may be less detectable, but they may also be in a cooler microclimate or represent a greater danger to the incubating parent if an obstructed view allows it to be ambushed by predators. Different types of predators may also require different forms of concealment (e.g. Burhans & Thompson, 2001). One would thus expect nest placement to be responsive to the nature of the predatory environment among other factors (see also Götmark *et al.*, 1995). It is also conceivable that frequency dependence will exist in the value of choosing one nest site over another in a given population of breeding birds.

As in many other areas of this review, very little 'ecological time' work exists regarding nest concealment. There are nevertheless some relevant studies (see also Martin, 1992a). Birds are known to shift to safer but cooler nest sites with an increase in nest predation risk (Marzluff, 1988; Eggers *et al.*, 2006). Furthermore, Wiebe & Martin (1998) suggested that concealed nests of white-tailed ptarmigan experienced less predation, but were also associated with greater female vulnerability to mammalian predators. This is precisely the sort of trade-off envisioned by Götmark *et al.* (1995). A similar trade-off may exist in Kentish plovers (*Charadrius alexandrinus*) deciding whether to nest in open *versus* partially vegetated areas (Amat & Masero, 2004). Based on comparative work, Weidinger (2002) suggests that species which can do little to defend against predators will gain the most from nest concealment; this might hold over ecological time when birds are faced with diverse predators against whom their defences vary.

Some counter-intuitive observations indicate that parents can compensate behaviourally for the lack of nest concealment (e.g. Cresswell, 1997; Remeš, 2005), although the nature of such parental behaviour has rarely been studied (but see Burhans, 2000; Burhans and Thompson, 2001).

Studies using artificial nests usually show that better concealment does lead to lower predation (Martin, 1992a; see also Weidinger, 2002; Remeš, 2005), but studies using natural variation in nest concealment often show no such effect (e.g. Götmark *et al.*, 1995; Howlett & Stutchbury, 1996; Cresswell, 1997; Burhans & Thompson, 2001; Remeš, 2005; see also Martin, 1992a). This lack of an effect of nest concealment also holds for studies that have experimentally removed vegetation around live nests (Howlett & Stutchbury, 1996; Peak, 2003). It thus appears that some aspect of parental decision-making can compensate for the loss of nest concealment. However, the existence of such compensation does not imply that nest concealment is an unimportant issue or that important trade-offs are not involved in determining a level of nest concealment (e.g. Howlett & Stutchbury, 1996; see also Fontaine *et al.*, 2007). A cost of compensating for less nest concealment may be expressed in ways such as a reduction in nesting feeding rate. Studies focused on the nature of these behavioural changes should yield insights into the trade-offs involved in nest placement and concealment.

(5) Nest construction

A bird could conceivably change the construction of its nest based on the perceived risk of predation. This possibility has received little attention, perhaps reflecting the fact that nest building is largely instinctive (Collias & Collias, 1984; Hansell, 2000). However, nest building is responsive to building experience and to changing thermal conditions (Collias & Collias, 1984; Hansell, 2000), and thus might also respond to changes in the risk of predation in ecological time (but see Møller, 2006).

A few experiments suggest ways in which nest construction might respond to changes in predation risk. Using natural European blackbird nests of various sizes, Møller (1990b) found that larger nests (containing plasticine eggs) suffered higher predation than did smaller ones. Similar results were obtained using artificial (Sieving & Willson, 1998) and natural nests (Antonov, 2004; López-Iborra *et al.*, 2004; but see Slagsvold, 1989; Weidinger, 2004). If smaller nests provide less insulation than larger nests (e.g. Slagsvold, 1982), then birds might construct smaller nests mainly when the perceived risk of nest predation is higher. Using experimentally constructed nests, Møller (1987) showed that open cup nests lined with more feathers (better insulated) were more prone to predation. As with nest size, it is conceivable that the feather content of nests could vary with the risk of nest predation. These sorts of predictions are experimentally testable.

(6) Routes to assessing the risk of nest predation

Any prediction of flexibility in response to the risk of nest predation assumes that birds can assess this risk somehow. There are potential sources of information about such risk, but as with the perception of risk in general, there are few relevant studies (Lima & Steury, 2005). However, it is worth considering cues that might be available to birds regarding classes or types of nest predators.

Obviously, sightings of potential nest predators will be a useful cue, although direct observations of nest predation would be more informative than sightings alone. Several studies on protector species associations in the Arctic suggest that birds may assess the diet of key predators (protectors) by assessing the density of small rodents (e.g. Ebbinge & Spaans, 2002), but this remains largely conjecture. Vocalizations might also be used to determine the presence of nest predators, as was shown experimentally by Eggers *et al.* (2005); this would probably apply mainly to avian predators, but also to vocal mammals such as squirrels (Schmidt and Ostfeld, 2008). Direct experience with nest predation *per se* is clearly a cue to disperse to a new location (see above), although it is unclear whether the identity of the predator was known to the dispersing birds (but see Hakkarainen *et al.*, 2001 and Thompson 2007). Shell fragments indicating prior nest predation might provide clues to the safety of possible nest cavities, but these do not deter female common goldeneyes from using a given cavity (Pöysä, 2003).

The presence of mammalian predators such as small rodents might be determined from their urine trails, which are detectable *via* the ultraviolet spectrum visible to birds (Viitala *et al.*, 1995). Olfactory detection abilities are probably relatively weak in birds, however. (Roper, 1999). A recent experiment (Godard, Bowers & Wilson, 2007) indicates that eastern bluebirds (*Sialia sialis*) do not avoid nest boxes containing the faeces of snakes or mice. However, a very similar experiment indicates that blue tits (*Cyanistes caeruleus*) recognize and avoid the scent of weasels in nest boxes (Amo *et al.*, 2008). Roth, Cox & Lima (2008) found that the vigilance of feeding house finches (*Carpodacus mexicanus*) increases in the presence of cat faeces and urine. Birds may thus have some ability to detect nest predators chemically, but it seems likely that the olfactory information available to them will not match that available to mammals and especially to aquatic animals (Kats & Dill, 1998; Chivers & Smith, 1998; Lima & Steury, 2005).

Snakes are a major nest predator of many types of birds, but they are quiet and may not be detectable (to birds) *via* olfaction (Godard *et al.*, 2007). Misenhelter & Rotenberry (2000) found that sage sparrows may not be able to assess differences in snake-driven nest predation across habitats, and perhaps this will prove to be a general result.

Finally, there is growing evidence that birds may obtain knowledge about the breeding success of not only their neighbours (e.g. Julliard *et al.*, 1997; Danchin *et al.*, 1998; Hoover, 2003; Citta & Lindberg, 2007) but also of birds much more distant (Parejo *et al.*, 2007). Doligez *et al.* (2004) suggest that birds actively seek out such information *via* prospecting trips and use it to decide where to attempt to settle in the next breeding season. This sort of public information (Seppänen *et al.*, 2007; Valone, 2007) is indeed valuable since it provides a direct measure of nesting success in a given location rather than an indirect cue of risk, assuming that there is predictability in nest predation across seasons (Citta & Lindberg, 2007). This is worthy of further investigation, keeping in mind that prospecting itself might be a risky behaviour (Addison, Ydenberg & Smith, 2007).

(7) Nest defence and visitation under variable predation risk

Decisions made about nest defence are inherently an ecological-time phenomenon. For instance, the risk to the nest and/or parent changes continuously as the predator approaches the nest, and as the parent responds. Decision-making in nest defence has been an active area of study for over 25 years. Montgomerie & Weatherhead (1988) provided a thoughtful and still relevant discussion of this literature, which was recently updated by Caro (2005). I will not duplicate these reviews here, although it is worth briefly summarizing the basic conclusions reached by Caro (2005), after which I consider related behavioural issues.

Work on nest defence has long been motivated by parental investment theory (Montgomerie & Weatherhead, 1988), with special reference to the way in which the intensity of defence changes with the value or quantity of offspring. It is clear that defending parents are sensitive to the degree of threat to themselves (e.g. Buitron, 1983; Curio, Klump & Regelman, 1983; Dale, Gustavsen & Slagsvold, 1996) and to their eggs/nestlings (e.g. Ghalambor & Martin, 2000, 2001). Caro (2005) notes that many studies indicate that nest defence increases as the young age and become more valuable to parental fitness, but that this is not uniformly the case (e.g. Dale *et al.*, 1996). There is ambiguous support for an increase in nest defence with the size of the brood or with offspring condition (Caro, 2005). Many of the complicating factors outlined in Montgomerie and Weatherhead (1988) still affect this field (Caro, 2005), but the overall pattern and interpretation seems clearer now than 20 years ago. There are still few studies that actually document the risks taken by parents in defence of young (but see Samelius & Alisauskas, 2006).

An area that has received much less attention is the way in which nest defence (or, more generally, nest guarding) interacts with other aspects of decision-making. For instance, the need to remain near the nest under higher risk situations may affect foraging tactics, incubation schedules, and temporal patterns in nest visitation. In an early study of nest defence, Martindale (1982) developed a central-place foraging model which included the costs and benefits of nest defence. Consistent with model predictions, following the appearance of a threat at the nest, male gila woodpeckers (*Melanerpes uropygialis*) increased foraging visits to patches closer to the nest. Hakkarainen *et al.* (2002) observed a similar effect in pied flycatchers (*Ficedula hypoleuca*). Similarly, following the witnessed loss of a nestling to a crow, a pair of pinyon jays spent more time gathering food close to the nest (Marzluff, 1985).

The above studies deal with cases in which parental defence of the nest can be effective; where this is not the case, different behaviors might be expected. For example, Siberian jays cannot effectively defend their nests against larger corvids; jays nesting in naturally high-risk areas tend to avoid feeding nestlings during the afternoon, when the threat of nest predation is highest (Eggers *et al.*, 2005; Eggers, Griesser & Ekman, 2008). This temporal pattern in visitation could be induced experimentally using playbacks of recorded predator calls (Fig. 4). These jays clearly avoided

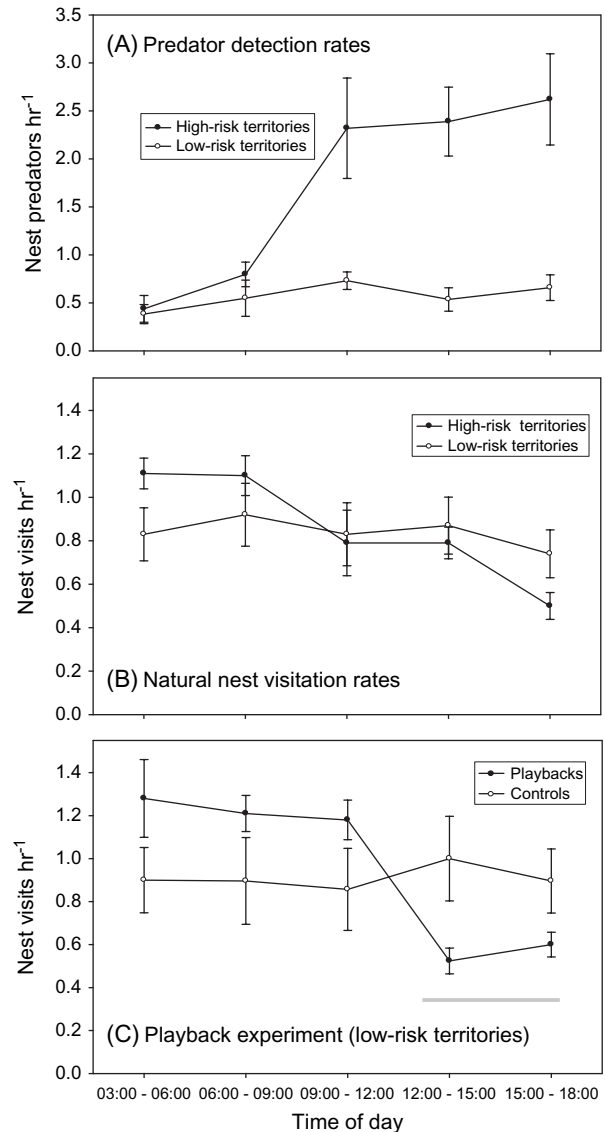


Fig. 4. Nest predators and their influence on nest visitation by Siberian jays (*Perisoreus infaustus*) in northern Sweden. The abundance of nest predators (A) peaked after noon at high-risk territories but remained relatively low and constant in low-risk territories. Natural nest visitation rates (B) mirrored the trends in predator abundance. Specifically, nest visitation rates were relatively unchanged across the day in low-risk territories, whereas visitation was higher in earlier portions of the day in high-risk territories. Playbacks of corvid nest predator calls during the afternoon (C) in low-risk territories had the effect of shifting nest visitation to earlier periods, much as seen in the natural nest visitation data. The horizontal bar indicates the timing of playbacks. Values are means \pm S.E.M., and all main treatment effects shown are significant (see Eggers *et al.*, 2005). Modified from Eggers *et al.* (2005).

revealing the location of the nest, and presumably devote more time to self-feeding and other competing activities when they are avoiding nest visitation. By contrast, food deliveries to nestlings by speckled warblers (*Chthonicola*

sagittata) appear to be unrelated to nest predation measured in the field (Gardner, 2007), although the identity of the nest predators was not known.

Lengthy bouts of incubation might represent nest guarding, whether to enhance nest concealment or to avoid attracting attention to the nest *via* entries and exits (Weathers & Sullivan 1989). Such an interpretation is suggested by a recent study unique in its scale (Fontaine & Martin, 2006*b*). A large-scale removal of nest predators led to a reduction in time spent incubating by females of several species, in concert with an across-species increase in feeding visits to the nest. This ecological-time response nicely complements a similar effect seen in a comparative study by Martin & Ghalambor (1999). Similarly, female lapwings (*Vanellus vanellus*) are more likely to be incubating eggs during periods when encounters with nest predators (magpies) are more common (Sasvári & Hegyi, 2000). In other systems, an increase in food abundance can lead to more time available for nest incubation or guarding, and thus a reduction in overall nest predation (Komdeur & Kats, 1999; Rastogi, Zanette & Clinchy, 2006; see also Martin, 1992*b*). In some cases, increases in nest guarding may be achieved at a cost to parental body condition if guarding must be carried out over long periods (e.g. Komdeur & Kats, 1999), but such effects have rarely been studied.

(8) Behavioural decisions made by nestlings

Nestlings are clearly very vulnerable, but they probably have some ability to make predation-risk-informed decisions in threatening situations. Such behavioural decision-making is perhaps unsophisticated, since nestlings undoubtedly have little direct experience with predators. There are nevertheless a few ways in which nestlings might manage their risk of predation *via* flexible decision-making.

(a) Threatening encounters

Newly hatched altricial young have no ability to avoid predators, but older nestlings may have some capacity to comprehend and avoid dangerous situations (Dor *et al.*, 2006). For most nestlings, there would seem to be only two options during a threatening encounter with a predator: stay very still, quiet, and low in the nest, or abandon the nest and scatter (if sufficiently ambulatory). If dangerous encounters happen when parents are present, the chicks may be directed to abandon the nest (Marzluff, 1985). Parental calls to silence the chicks are also known in several species (see Platzen & Magrath, 2004; Caro, 2005; Magrath, Pitcher & Dalziell, 2007). However, dangerous encounters may happen in the absence of parents. The first response of unprotected nestlings will likely be to become silent and lie low in the nest. Nest abandonment is likely to occur only when capture is imminent.

Marzluff (1985) describes a particularly relevant case of nest abandonment in an encounter between advanced pinyon jay nestlings and a crow (*Corvus brachyrhynchos*). The crow was in the nest and striking at the nestlings, yet they

did not abandon the nest until their parents appeared and gave an apparent command. Similarly, advanced nestling moustached warblers (*Acrocephalus melanopogon*) did not abandon the nest with the close approach of a predator, but rather remained silent (Kleindorfer, Hoi, & Fessl, 1996); here too, the chicks did not abandon the nest until their parents directed them to do so. Perhaps young birds are generally reluctant to abandon the nest on their own, although hoatzin (*Opisthocomus hoazin*) chicks readily abandon the nest in threatening situations (Strahl, 1987).

(b) Begging

Begging by nestlings can attract the attention of predators (Leech & Leonard, 1997; see also below), and this may be a key area in which decision-making by chicks could influence nest predation. One could imagine situations in which chicks alter their begging in dangerous environments, or attempt some sort of trade-off in begging behaviour. Comparative work suggests that the nature of the begging calls themselves has been shaped by predation (Redondo & de Reyna, 1988; Briskie, Martin & Martin, 1999), and perhaps nestlings can alter their begging calls in ecological time as well. I know of no work addressing the existence of such predator-induced flexibility in begging calls, but chicks are known to alter their calling in response to environmental noise (Leonard & Horn, 2008).

An important question related to flexibility in begging is whether nestlings can differentiate low- and high-risk situations while in the nest. Perhaps the best rule is to beg loudly when a parent appears, since it has presumably assessed the immediate absence of predators before approaching the nest. Information about local risk will exist in the form of the frequency with which nestlings receive alarm calls from their parents (see Caro, 2005; Magrath *et al.*, 2007). Non-lethal encounters (visual sightings, etc.) with predators might also add to a perception of risk in nestlings. Nestlings of an Australian scrubwren (*Seticornis frontalis*) respond with prolonged silence to playbacks of sounds made by a walking corvid predator (Magrath *et al.*, 2007), although the role of experience here is unknown (see also Grodzinski, Erev & Lotem, 2008).

It seems likely that nestlings are capable of striking some sort of flexible, ecological-time trade-off between the risk of predation and the demands of competitive begging. This is also suggested by the fact that (i) hungry nestlings are relatively more likely to beg in response to potentially dangerous stimuli (see Leonard, Thorn & Mukhida, 2005), and (ii) begging calls change to some extent (both in intensity and quality) in response to hunger (Dickens & Hartley, 2007; Magrath *et al.*, 2007). Such state-dependence in behaviour is a foundation of flexible behavioural trade-offs (Mangel & Clark, 1988; Houston & McNamara, 1999). Interestingly, nestling responsiveness to inappropriate stimuli decreases with nestling age (e.g. Moreno-Rueda, 2005; Dor *et al.*, 2006; but see Leonard *et al.*, 2005), suggesting an improvement in the cognitive abilities of older nestlings.

III. PREDATION ON ADULTS AND CHOICE OF BREEDING SITE

Obviously, a breeding bird's fitness is dependent on its own survival, and certain breeding locations must be safer than others from an adult's point of view. Such considerations probably influence the choice of breeding site in many species. An ability to avoid *Accipiter* hawks and falcons, the most dangerous predators faced by most adult birds, would be advantageous, but it might be difficult to avoid such mobile predators, who could simply distribute themselves such that most breeding birds are subject to similar risk (Lima, 2002; Sih, 1998; MacLeod *et al.*, 2007). However, such avian predators are spatially "anchored" to their own nesting sites during the breeding season, thus establishing spatial patchiness in predation risk, especially when combined with predator territoriality. Further patchiness in risk may occur when predators are limited to nesting in certain landscape features such as cliffs, *etc.* Hence in many cases it ought to be possible for adult birds to avoid dangerous predators to some extent *via* choice of breeding site.

Compared to work on nest predation, only a few studies have addressed the issue of predation on adults (Table 1). All are based on the premise that risk to adults declines as distance to a raptor's nest increases. An avoidance of nesting in the proximity of hawk and falcon nests is generally observed (Table 1). Such avoidance can extend several hundred meters from raptor nests (Fig. 5).

Not all species appear to avoid hawk nests, perhaps depending on whether they are a component of the hawk's diet; several studies suggest that species that are not the focus of predation do not avoid raptor nests (e.g. Suhonen, Norrdahl & Korpimäki, 1994; Mönkkönen *et al.*, 2007; but see Sodhi, Didiuk & Oliphant, 1990; Meese & Fuller, 1989). Interestingly, Suhonen *et al.* (1994) found the best evidence of such avoidance in migratory species that arrived after the raptor (kestrels, *Falco tinnunculus*) had already established their nest sites (Fig. 5). Permanent residents were unable or unwilling to relocate after a kestrel established a nest nearby (see also Fontaine & Martin 2006a). A similar effect might explain why willow tits (*Poecile montana*, a permanent resident) did not avoid sparrowhawk (*Accipiter nisus*) nests

Table 1. Influence of predation risk experienced by adult birds on their choice of territory or nesting site, as expressed by avoidance of areas near raptor nests.

Predator	Focal breeders	Avoidance	Comments	Reference
Sparrowhawk (<i>Accipiter nisus</i>)	blue tit, great tit	Yes	Clear avoidance of area within 60 m of hawk nests, but not beyond that distance.	Geer (1978)
Peregrine falcon (<i>Falco peregrinus</i>)	Arctic breeding passerines	Yes/No	Three of four species show avoidance within 400 – 700 m of falcon nest. The fourth was apparently constrained to nest near falcon due to nest site requirements.	Meese & Fuller (1989)
Merlin (<i>Falco columbarius</i>)	mainly urban passerines	Yes	Community-wide avoidance of falcon nest up to approximately 250 m.	Sodhi <i>et al.</i> (1990)
European kestrel (<i>Falco tinnunculus</i>)	passerines in agricultural habitat	Yes/No	Community-level measure of avoidance; effect apparent mainly in migratory species that establish territories after the arrival of kestrels, and in species < 140 g. Avoidance apparent at least to 1 km from kestrel nests.	Suhonen <i>et al.</i> (1994)
European kestrel	passerines in agricultural habitat	Yes	Verified that the avoidance effect seen in Suhonen <i>et al.</i> (1994) was not due to predator removal of prey; also demonstrated significant avoidance in individual species.	Norrdahl & Korpimäki (1998)
Great grey shrike (<i>Lanius excubitor</i>)	small, open-habitat passerines	Yes/No	Avoidance apparent at community level, but significant in only two species (with adequate data).	Hromada <i>et al.</i> (2002)
Sparrowhawk	willow tit	No	Hawks chose territory after prey territories already established; characteristics of offspring varied as a function of distance to hawk nest.	Thomson <i>et al.</i> (2006a)
Sparrowhawk	pie'd flycatcher	Yes	Avoidance of nest boxes within approximately 400 m of hawk nests.	Thomson <i>et al.</i> (2006b)
Goshawk (<i>A. gentilis</i>)	mainly boreal passerines	Yes/No	Avoidance of hawks by preferred prey species; smaller (less preferred) species tended to be more abundant closer to hawk nests, possibly as protection against nest predation.	Mönkkönen <i>et al.</i> (2007)
Eagle owl (<i>Bubo bubo</i>)	tawny owl (<i>Strix aluco</i>)	Yes	Large-scale spatial avoidance most apparent at intermediate density of eagle owls; tawny owls may only be able to avoid areas frequented by hunting eagle owls when the latter nest at higher densities.	Sergio <i>et al.</i> (2007)

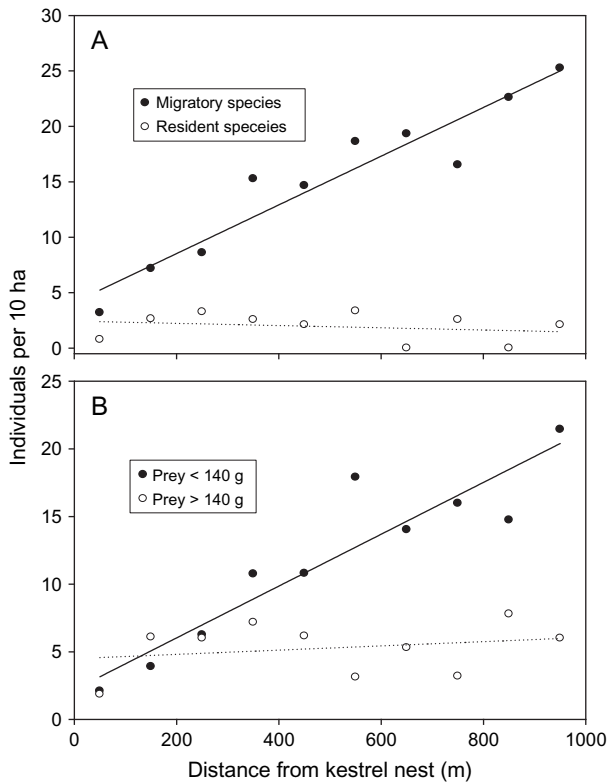


Fig. 5. Effect of distance from kestrel (*Falco tinnunculus*) nests on small bird abundance as a function of their (A) migratory status, and (B) body size, at a site in Finland. Most migratory species arrive after kestrels begin nesting, and thus have the opportunity to avoid nesting near kestrels. Smaller (and more vulnerable) species also tend to avoid nesting near kestrels. Solid regression lines are significant at $P < 0.001$, whereas dashed regression lines are not significant ($P > 0.40$). The avoidance of kestrel nests extended to a distance of at least 1 km. Data were pooled over several transects and species. Modified from Suhonen *et al.* (1994).

(Thomson *et al.*, 2006a) even though the migratory pied flycatcher clearly did (Thomson *et al.*, 2006b). However, this reasoning does not explain why only two species seemed to avoid great grey shrike (*Lanius excubitor*) nests in a different system (Hromada, Tryjanowski & Antczak, 2002), since the shrikes began breeding before most other birds established their territories; shrike diet was not examined. An apparent positive association between the nests of peregrine falcons and snow buntings (*Plectrophenax nivalis*) in western Greenland (Meese & Fuller, 1989) appears to reflect the lack of suitable (rocky) bunting nesting sites away from the cliffs preferred by the falcons.

Almost all of the studies cited in Table 1 are observational, and as such are subject to certain limitations. Chief among these is patchiness in landscape or habitat features that might confound interpretations of negative or positive associations between predator and prey (e.g., Meese & Fuller, 1989). Ideally, study site habitats should be as uniform as possible, such as the uniform agricultural landscape used by Suhonen *et al.* (1994). Clearly, an ability

to manipulate the presence of raptors would be valuable, but that was impossible in most systems studies (Table 1), except those involving cavity-nesting kestrels (Suhonen *et al.*, 1994; Norrdahl & Korpimäki, 1998).

Predator avoidance by adults may also have effects at scales other than those illustrated in Table 1. For instance, nest site choice by Kentish plovers appears to reflect a small-scale trade-off between thermally favourable (shaded) nesting spots and a greater ability to detect ambush predators in exposed sites (Amat & Masero, 2004; see also Wiebe & Martin, 1998 and Section II.4). Taking a different perspective, Sergio *et al.* (2007) argue that avoiding the nests of large owls may not be viable when these predators are relatively abundant; under such circumstances, it might be best to avoid habitats frequented by these owls in search of their preferred (mammalian) prey.

IV. PERSPECTIVES ON SOCIALITY DURING THE BREEDING SEASON

Work on sociality during the breeding season has traditionally focused on colonially-breeding birds, for whom the anti-predator benefits of sociality were thought to underlie coloniality itself (see Lack, 1968). There are indeed several studies suggesting that coloniality deters nest predators (Hoogland & Sherman, 1976; Götmark & Andersson, 1984; Robinson, 1985; Brown & Brown, 1987; Picman, Pribil & Isabelle, 2002), but several comparative studies suggest that predation is not a major driving force behind coloniality (Clode, 1993; Danchin & Wagner, 1997; Wagner *et al.*, 2000; Varela, Danchin & Wagner, 2007). Much of this work is comparative in nature, since coloniality tends to be a species-specific trait. Thus, the role of predation in shaping coloniality largely falls outside the scope of this review, although some of the literature on colonial species is relevant here (e.g., Beletsky, Higgins & Orians, 1986; Hogstad, 1995).

My less traditional starting point is a prominent behavioural feature of the avian breeding season: the breakdown in sociality across a variety of species (especially temperate-zone passerines). This breakdown is notable since non-breeding birds often reduce the risk of predation *via* flocking (Krause & Ruxton, 2002; Beauchamp, 2003; Caro, 2005). Birds in flocks are safer for several reasons (Cresswell, 1994a; Roth & Lima, 2003; Roth, Lima & Vetter, 2006), including the early warning of attacks afforded by collective vigilance (Elgar, 1989; Roberts, 1996; Bednekoff & Lima, 1998; Beauchamp, 2003; see also Caro, 2005). Birds without access to flocks can suffer loss of body condition and fitness (Dolby & Grubb, 1998). Do classically territorial breeding birds have no such need for social predator avoidance?

It seems unlikely that a transition to territoriality from sociality reflects a general reduction in predation risk during the breeding season. *Accipiter* hawks are often present during the breeding season (Post and Götmark, 2006a,b; Möller *et al.*, 2006), and indeed these hawks may represent an even greater risk at that time since they have their own offspring

to feed. Perhaps sociality is less effective during the breeding season due to visual obstruction by vegetation, although the re-establishment of flocking during late summer after breeding has ceased (e.g., Morse, 1970) argues against this interpretation (see also Ryabitshev & Tarasov, 1994). The transition back to flocking has not been well characterized in any system, but it can begin as early as late June in south-central Canada (Hobson and Van Wilgenburg, 2006) and elsewhere (Morse, 1970). Perhaps territoriality simply provides priority access to a stable food supply and nesting sites required for successful reproduction (Gill, 2007), and these benefits offset the costs of increased predation risk. Territoriality may also reduce density-dependent nest predation *via* the spacing of nests (see Section II.3). A major cost of sociality during the breeding season is sexual competition as reflected in extra-pair fertilizations (EPFs, Birkhead & Møller, 1992), and a serious loss of fitness *via* EPFs could conceivably outweigh any anti-predator benefits of sociality and select for territoriality (Møller, 1990a, 1992). Whatever the factors favouring territoriality, some forms of anti-predator sociality may nonetheless be maintained during the breeding season.

(1) Intraspecific anti-predator sociality during the breeding season

By definition, territorial birds are not likely to engage in sociality typical of the non-breeding season. There are nevertheless various behavioural phenomena which can reasonably be considered in the context of intraspecific flocking.

(a) *The mated pair as a flock of two*

In territorial species, the mated pair is probably the most predictable social grouping during the breeding season. The few studies in this area suggest that one member of the pair provides vigilance-related protection for the other. For example, Scheuerlein & Gwinner (2006) observed that a female stonechat was more likely to deliver food to the nest if her mate was nearby and vigilant, probably a good indication that no predators are nearby.

Other “flock of two” observations revolve around mate-guarding behaviour. A male guarding its mate is almost always assumed to be guarding its own paternity. A contrasting idea is that a guarding male may provide safety for a female, but a comprehensive review of avian mate guarding found little support for this (Birkhead & Møller, 1992). However, a series of papers on mate guarding in white-tailed ptarmigans provides possible counterexamples. Males of this species may spend much time vigilant when their mate is nearby and feeding (Martin, 1984), and male vigilance is higher when predator abundance increases (Artiss & Martin, 1995). Upon terminating a bout of incubation, the female often flies directly to her mate and feeds alongside him (Wiebe & Martin, 1997). Artiss, Hochachka & Martin (1999) suggest that the male’s vigilance behaviour allows a female ptarmigan to feed much more quickly than she would otherwise. Furthermore,

this vigilant mate guarding extends well into incubation, i.e. after fertilization takes place. More recently, Squires, Martin & Goudie (2007) found that male harlequin ducks (*Histrionicus histrionicus*) are more vigilant around their mates, especially when both are feeding in riskier habitats close to shore. This vigilance appears to allow females to feed at a higher rate than they would otherwise. Collectively, these studies make a reasonable case for males guarding the safety of their mates, although such observations do not rule out a simultaneous role for paternity assurance.

(b) *Social auditory signaling about risk between members of a pair*

Breeding male passerines can be particularly vocal, and such vocalizations might communicate information about the predatory environment to their mates. This idea is related to Wickler’s (1985) “watchman’s song” hypothesis, in which frequent vocalizations can function as an “all clear” signal. This hypothesis has not received much attention, but a growing number of studies suggest that perhaps it should.

Several studies indicate that incubating females time nest departures to occur shortly after their mates begin bouts of singing from a nearby location. Such singing could act as an all-clear signal, since a male would presumably not sing in the presence of imminent danger. Nest departures by female great tits (*Parus major*) occur shortly after males begin singing near the nest cavity (Lind, Dabelsteen & McGregor, 1996), and they often forage alongside the male. Mace (1987) suggested that singing in the dawn chorus functions to call out females early for copulation, but as Lind *et al.* (1996) point out, singing occurs throughout the day and is not necessarily associated with copulation. Female house wrens (*Troglodytes aedon*) show a strong tendency to terminate incubation and leave nests shortly after males begin singing; if a male is removed temporarily, incubation bouts by females increase by about 20 % (Ziolkowski *et al.*, 1997; see also Johnson & Kermott, 1991). Female reed buntings (*Emberiza schoeniclus*) also tend to terminate bouts of incubation when males initiate singing (Wingelmaier, Winkler & Nemeth, 2007). Møller (1992) extended this effect to communication among local males (both conspecific and heterospecific) *via* the observation that song playbacks often induced males of several species to begin singing, perhaps due to an all-clear effect.

A unique set of studies on vocal signaling in red-winged blackbirds (*Agelaius phoeniceus*) indicates that males act as sentinels for females much as envisioned by the watchman’s song hypothesis (Wickler, 1985). Beletsky *et al.* (1986) showed that males give continuous short, sharp calls, and that changes in the call types indicate heightened risk nearby, and cause females to become more vigilant (Beletsky, 1989). Females are more likely to terminate incubation (to feed, *etc.*) when their mates are present and calling (Burton & Yasukawa, 2001), and females are also more vigilant when they cannot hear their mate’s calls (Beletsky, 1989). Beletsky (1991) showed that males call at higher rates as a human approached the nest, or when a stuffed predator (owl or magpie) was placed close to the nest. This graded auditory signaling of risk is similar to that

seen in pairs of Carolina wrens (*Thryothorus ludovicianus*), but the female wrens do most of the vocalizing (Morton & Shalter, 1977).

(c) *Diffuse intraspecific anti-predator sociality in territorial birds*

Many bird species exhibit strong intraspecific territoriality, but they may nevertheless engage in anti-predator behaviour at a distance *via* alarm calls that (perhaps inadvertently) alert them to danger, perhaps followed by some sort of joint defensive behaviour. This I term a sort of diffuse anti-predator sociality. Such interactions might conceivably affect the spacing of territories according to the degree of risk in the local environment (see also Myers 1980). Arguing against this idea are studies suggesting that territories of passerines often expand to fill the available space and thus are as far apart as possible (e.g. Smith *et al.*, 2006). However, such studies do not directly address the key issues here.

Perhaps the most obvious form of diffuse anti-predator sociality would be distinct clusters of territories in which birds communicate in some way about predators and benefit accordingly. A possible example occurs in least flycatchers (*Empidonax minimus*), which often nest in clusters of territories that are not obviously associated with various environmental features (Perry & Andersen, 2003). Birds in these clusters seem to respond to the alarm calls of neighbours with joint mobbing of predators (Perry & Andersen, 2003), and territories in the interior of clusters experience lower nest predation (Perry, Manolis & Andersen, 2008). However, Tarof & Ratcliffe (2004) could find no clear benefit of such clusters with regard to nest predation. Furthermore, Tarof *et al.* (2005) examined extra-pair fertilizations in such clusters and suggested that these clusters function as “hidden leks”: socially monogamous males set up adjacent territories in a lek-like fashion to secure extra-pair matings (see also Fletcher & Miller, 2006). This is an intriguing idea, and one that is not mutually exclusive to an anti-predator function of such clusters.

Another case for a diffuse anti-predator warning system can be found in the above-mentioned vocal warning system of red-winged blackbirds (Beletsky *et al.*, 1986). These calls are omnidirectional and broadcast widely (Patricelli, Dantzker & Bradbury, 2007), and are thus available to all red-wings in the area. Beletsky *et al.* (1986) showed that nearby males perceive sudden call transitions as indicators of a threat. Hence this warning system appears shared in some sense among adjacent males, much as is visual vigilance in flocking birds.

(2) Heterospecific sociality in breeding birds

Territorial birds may be physically distant from conspecifics, but heterospecific birds may often be nearby with overlapping territories. Such heterospecific neighbours provide a social basis for reducing predation risk. In fact, given a general reluctance to cross intraspecific territorial boundaries (Betts, Hadley & Doran, 2005; but see also Olendorf, Getty & Scribner, 2004), such social interactions may often be limited to heterospecifics. There are also cases

in which heterospecific associations are negative, at least for one of the species involved (see Martin & Martin, 2001; Forsman, Thomson & Seppänen, 2007 and references therein).

(a) *Heterospecific flocking*

Heterospecific flocking is prominent during the non-breeding season (Morse, 1970, 1977; Caro, 2005), and tropical mixed-species flocks occur during the breeding season, although in a diminished form (Greenberg, 2000; Tubelis, 2007). By contrast, heterospecific flocking in temperate environments, if it exists, is not as obvious as that seen during the non-breeding season. However, more subtle forms of flocking may exist.

This phenomenon has been explored in a series of papers on small birds breeding in the boreal forests of northern Europe. Mönkkönen, Forsman & Helle (1996) found that foraging passerines tended to be heterospecifically clumped in their small-scale distributions, with about half of observed birds feeding within 15 m of a heterospecific individual. Parids appeared to be the preferred associates, much as they are in the non-breeding season (Morse, 1977; Smith, 1991; Caro, 2005). Furthermore, a playback experiment using the territorial song of willow tits attracted a variety of heterospecifics, presumably looking for a flocking partner. A similar study found a reduction in nearest-neighbour distances (by about 20 m) among foraging birds following simulated encounters with predators (Forsman *et al.*, 1998). The birds were still fairly far apart, at about 30–50 m, and thus did not form tight heterospecific flocks, but anti-predator benefits may nevertheless have resulted. Species identity unfortunately was not considered by Forsman *et al.* (1998). Perhaps some of the benefits of heterospecific associations in these boreal systems reflect the benefits of heterospecific mobbing rather than the standard feeding and early-warning benefits (Krause & Ruxton, 2002) of flocking *per se*. For instance, Forsman, Seppänen & Mönkkönen (2002) found that pied flycatchers nesting in close association with resident parids gained a substantial reproductive advantage; the precise mechanism underlying this advantage was not identified (see also Seppänen, Mönkkönen & Forsman, 2005; Forsman *et al.*, 2007), but heterospecific neighbours are frequent mobbing partners during encounters with predators (Forsman & Mönkkönen, 2001). In a different boreal system, Krams & Krama (2002) found much heterospecific mobbing, but only after various species had been settled in a given area for a while.

(b) *Protector species associations*

The formation of protector species associations (see Caro, 2005 for a review) often represents an ecologically flexible form of heterospecific sociality. As mentioned earlier (Section II.2b), a protector species’ aggressive defence of its own nest is used by members of other species to cover the defence of their nests as well. In fact, the protected species usually leave nest defence to the protector (e.g., Bogliani *et al.* 1999; Larsen, 2000). It is tempting to classify this relationship as parasitic, but only Groom (1992) provides evidence for such an effect (involving a nighthawk protectee

and larid protectors). Some of these relationships may be largely obligate for the species seeking protection (e.g. Groom, 1992; Quinn *et al.*, 2003), but most appear to be facultative (e.g., Bogliani *et al.*, 1999) and thus are potentially flexible in response to changes in nest predation risk.

Flexibility in associations with protector species stems from the fact that many “protector” species, at least the more effective ones, are potential threats to the protected. For instance, brent geese (*Branta bernicla*) nesting the high Arctic prefer islands with gulls for nesting (see Ebbinge & Spaans, 2002), and so avoid nest/offspring predation by foxes. However, in years with many lemmings (*Lemus* and *Dicrostonyx* spp.), some of these small geese nest on the mainland in close proximity to snowy owl nests. These owls focus almost entirely on lemmings during such years, and are effective at driving away foxes. Geese nesting in association with the owls thus avoid potential nest predation by both foxes and gulls, and may enjoy a better feeding environment. Larsen (2000) describes a similarly flexible, rodent-density-dependent association between bar-tailed godwits (*Limosa lapponica*) and their protector species. In low rodent (lemming) years, the godwits associate with whimbrels (*Numenius phaeopus*) or grey plovers (*Pluvialis squatarola*; Larsen & Grundetjern, 1997). During high lemming years, the godwits also associate with long-tailed skuas (*Stercorarius longicaudus*), which are better nest defenders but also represent a threat to godwit chicks when not focused on lemmings. Many other protective arrangements are known (Caro, 2005), but such flexibility is not usually the focus of these studies.

These protective arrangements are interesting biological systems that are not yet well understood. The degree to which the above sort of flexibility exists is unclear, but possibly widespread. It would be useful to pursue additional cost-benefit work in these systems, with greater consideration of (i) the degree to which such associations are obligatory or subject to differing perceptions of predation risk, (ii) why many members of a population may not be in such relationships (e.g. Blanco & Tella, 1997; Bogliani *et al.*, 1999), and (iii) the degree to which these associations are genetically determined or subject to cultural learning for particular species. Additional work examining the geographical extent of such systems would also be useful: most known systems are in the Arctic, but a few temperate and tropical examples are known (Caro, 2005). Such protector systems may be more widespread than currently realized.

V. LIFE-HISTORY RESPONSES TO CHANGING RISK

The study of avian life histories usually concerns broad evolutionary patterns, and indeed the bulk of the diversity in avian life histories occurs among the deeper nodes of the avian phylogenetic tree (Bennett & Owens, 2002; see also Remeš & Martin, 2002; Martin 2004). Nevertheless, natural selection should favour some degree of plasticity in life history or reproductive traits expressed by individual birds, especially as they relate to variation in the risk of predation

on nestlings or adults (Lima, 1987; Clark & Ydenberg, 1990*a,b*, Ydenberg, 1994; Clinchy *et al.*, 2004). Such flexibility might involve changes in clutch size and parental decisions that influence the characteristics of offspring, or even the decision to engage in reproduction itself.

(1) To breed or not to breed

Perhaps the most basic demonstration of flexibility in reproduction would be the decision to forgo breeding (to assume a clutch size of zero) if the risk were deemed too high. Only relatively long-lived birds could presumably benefit from such a decision. Predation-induced breeding suppression has been suggested in small mammals, in which breeding is minimized in an effort to improve survival during periods of high risk; breeding occurs subsequently when conditions improve (Ylönen, 1994; Kokko and Ruxton, 1999). This idea is controversial in small mammals (Mappes, Koskela & Ylönen, 1998; see also Lima, 1998), but there are two examples known in birds, both in Arctic waterfowl. Spaans *et al.* (1998) found that brent geese forgo reproduction (egg laying) after frequent encounters with Arctic foxes (*Alopex lagopus*) during nest initiation. Similarly, Steller’s eiders (*Polysticla stelleri*) often forgo breeding during years with low lemming densities (Quakenbush *et al.*, 2004). These eiders appear to breed mainly in high lemming years when key protector species (snowy owls and skuas) are hunting abundant lemmings rather than other prey. There may be other species that show this “zero clutch size” response to a high-risk breeding season, but they are probably relatively few in number.

(2) Predation and flexibility in clutch size

There is a small body of work showing ecological-time flexibility in avian clutch size in response to changing predation risk. Here, it will be useful to distinguish between risk experienced by adults *versus* that experienced by eggs or nestlings, although the two are not always easy to separate.

(a) Risk to adults

Some models (e.g. Lima, 1987) suggest that an increase in predation risk experienced by adults should lead to a smaller clutch size in ecological time. Such a response would lead to less time foraging and thus less time exposed to predators. The fact that breeding adults face a considerable predation risk has been demonstrated in a variety of systems (Geer, 1978; Ainley & Masters, 1980; Harris, 1980; Watanuki, 1986; Nelson, 1989; Harfenist & Ydenberg, 1995; Post & Götmark, 2006*a,b*; see also Slagsvold & Dale, 1996), but a reduction in clutch size in response to increased risk to adults is not empirically well established. Only Thomson *et al.* (2006*b*), working with pied flycatchers nesting relatively close to sparrowhawk nests, provide evidence for such a decline in clutch size. The tendency of stonechats to forgo a second nesting attempt when shrikes are nesting nearby may also reflect a heightened risk to parents (Scheuerlein, Van’t Hof & Gwinner, 2001).

(b) Risk to nests

Some observational studies provide examples of adjustments in clutch size in response to an increased risk of nest predation. Julliard *et al.* (1997) found that an increase in weasel predation on great tit nests during a given year led to a one egg reduction in clutch size in nesting attempts the following year. Somewhat mysteriously, this reduction was also observed in birds that did not experience predation directly. These observations suggest that weasel predation in a given year indicates high risk in the next year, and that most of the tits were aware of the increased risk. Doligez & Clobert (2003) experimentally manipulated nest predation rate in the collared flycatcher. They simulated nest predation using model predator presentations followed by the removal of all nestlings from 20 – 35 % of active nests. This procedure resulted in a modest reduction in clutch size (0.2 eggs out of a typical clutch size of six) during the following year across the entire local population. Additional observational work on song sparrows (*Melospiza melodia*; Zanette, Clinchy & Smith, 2006) showed slightly lower average clutch sizes at predator-rich mainland sites relative to those from predator-free islands. A study on brent geese (Van Kleef *et al.*, 2007) found that those nesting closer to a protector (snowy owls) laid relatively larger clutches with larger eggs. Van Kleef *et al.* (2007) suggest that healthier geese are able to compete better for the safest spots closer to the owls, but the observed effects could conceivably represent flexible responses to the lower risk itself.

Two recent experimental studies provide particularly relevant but opposing results on nest predation and clutch size. Eggers *et al.* (2006) showed that, after experimental exposure to the taped calls of nest predators, Siberian jays laid clutches that were on average about 25 % smaller (a one egg drop) than typical clutch sizes. On the other hand, Fontaine & Martin (2006b) found no significant change in clutch size following the removal of nest predators in any of the many species that they studied (see also below).

A reduction in clutch size with increasing nest predation risk could reflect one of a few broad effects, which are not mutually exclusive. These have been suggested to explain interspecific patterns in clutch size among altricial species, but they may also apply to flexibility in ecological time. Skutch (1949) (see also Martin *et al.*, 2000a; Ferretti, Llambías & Martin, 2005) suggested that smaller clutch (or brood) sizes can be favoured under high nest predation levels when predators are attracted by parental visits to the nest or noise from begging young. It has been demonstrated experimentally that larger/noisier broods are more detectable to predators (Haskell, 1994; Leech and Leonard, 1997; Martin *et al.*, 2000b). Götmark (2002) showed that great tit fledglings from larger broods are more likely to become prey for sparrowhawks than are those from smaller broods (Fig. 6), an effect that he attributed to greater noise and/or parental feeding trips. Some studies (e.g. Roper & Goldstein, 1997) show that nest predation rates are not necessarily higher during the noisy nestling portion of the breeding cycle (as opposed to the egg period) as one might expect. However, Martin *et al.* (2000b), in a targeted analysis of nest predation found higher predation on nestlings than on eggs (see also

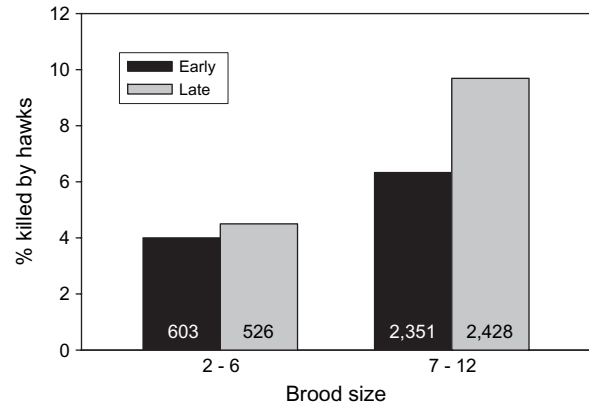


Fig. 6. Percentage of recently fledged great tits (*Parus major*), as a function of brood size and time-of-season, known to have been killed by sparrowhawks (*Accipiter nisus*) at a site in Sweden. Values are the overall percentages of banded birds recovered from sparrowhawk nests and plucking sites. Numbers at the base of bars represent total young banded. The vulnerability of fledged young increased significantly with brood size, especially for later breeding attempts. Modified from Götmark (2002).

Muchai & du Plessis, 2005). Fontaine & Martin (2006b) showed that nest visitation uniformly increased in areas where nest predators had been removed, lending further support to an ecological-time version of Skutch's hypothesis.

Birds can expect to lose one or more nests each season given typical levels of nest predation. As suggested by Slagsvold (1982, 1984), if the success of a subsequent nesting attempt is directly related to the investment in the previous attempt, then breeding birds facing high nest predation levels should lay smaller clutches in any given nesting attempt in order to reserve resources for future attempts. Which resources may be limiting across multiple nesting attempts is unclear, but key nutrients like calcium may well be significant.

A relatively recent model suggests that something more fundamentally strategic may explain the effect of nest predation on clutch size. Farnsworth & Simons (2001) modeled the optimal allocation of a given number of eggs over a given number of possible nesting attempts. The model is based on a trade-off between clutch size and total exposure to nest predation. Given this trade-off, it is best to spread eggs over multiple attempts in the face of high nest predation, even in the absence of any sort of resource limitation or increased detectability of large broods. This result resembles that from bet-hedging models of optimal reproduction (Gillespie, 1977), but the optimal strategy in the present case is one that simply maximizes mean reproductive success (see also Bulmer, 1984). The Farnsworth & Simons (2001) model also predicts the frequently observed decline in clutch size over the breeding season without reference to limited resources or poor prospects for late-hatched young; incorporating this model into one with explicitly flexible reproduction might prove insightful.

A potential problem for ideas relating predation risk to changes in clutch size is a result from the predator-removal

experiment of Fontaine & Martin (2006b). They found no change in clutch size following the removal of nest predators, but did show an increase in egg mass across nearly all species studied (Fig. 7). This result was not anticipated by existing theory, and clearly needs more theoretical and empirical attention. It is worth noting that the species studied by Fontaine & Martin (2006b) have relatively small clutches in which an additional egg might represent a prohibitively large increase in reproductive effort. Under such circumstances, perhaps larger eggs (representing a greater investment in each young) are a better option in the face of lowered risk.

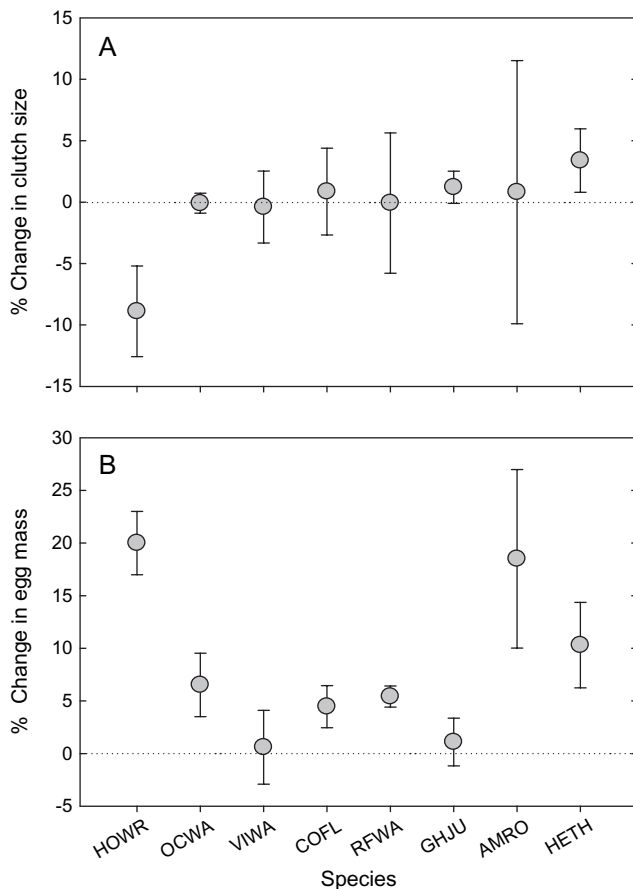


Fig. 7. Effects of nest predator removal on (A) clutch size and (B) egg mass for eight passerines from several study sites in northern Arizona, USA. Values are means \pm S.E.M.; positive values represent increases in response to predator removal. Dashed lines indicate 0 % change. Analysis by Fontaine & Martin (2006b) indicates that predator removal had no significant effect on clutch size, and a significant effect on egg mass (with a significant treatment \times species interaction). Species codes are as follows (HOWR - house wren (*Troglodytes aedon*); OCWA - orange-crowned warbler (*Vermivora celata*); VIWA - Virginia warbler (*V. virginiae*); COFL - cordilleran flycatcher (*Empidonax occidentalis*); RFWA - red-faced warbler (*Cardellina rubrifrons*); GHJU - gray-headed junco (*Junco hyemalis*); AMRO - American robin (*Turdus migratorius*); HETH - hermit thrush (*Catharus guttatus*). Modified from Fontaine & Martin (2006b).

(3) Parental decisions and characteristics of offspring

A breeding bird can reduce its personal risk of predation by reducing foraging time and hence exposure to predators. This response will inevitably lead to a loss of body condition in its offspring and the ensuing fitness consequences (e.g. Lima, 1987; Ydenberg, 1994). Thus the costs of the risk experienced by foraging parents may largely impact on the nestlings (see also Mauck & Grubb, 1995), especially if that risk is chronically high and the parents are relatively long-lived. Such costs have been observed in a few studies, and it is likely that this situation is common to many avian systems.

Young birds fledge at lower body mass when parents are feeding in risky situations. In two separate studies, pied flycatchers fledging from nests relatively close to those of sparrowhawks were lighter and also somewhat smaller (Forsman, Seppänen & Mönkkönen, 2002; Thomson *et al.*, 2006b). In neither study was the overall effect very large, however. In rhinoceros auklets (*Cerorhinca monocerata*), adults terminated the feeding of their single offspring earlier when subject to greater predation from eagles near the nesting colony (Harfenist & Ydenberg, 1995). Auklet chicks in high-risk sites were thus forced to fledge earlier and lighter than those in low-risk sites (see also Ydenberg, 1989, 2001). Similarly, Atlantic puffins fledge lighter in colonies where parents run a gauntlet of greater black-backed gulls (*Larus marinus*; Harris, 1980). Velando & Márquez (2002) found that Inca terns nesting in more dangerous locations (far from a cliff edge) made fewer visits to their nests, with a correspondingly large effect on chick body mass (Fig. 8). For stonechats (Scheuerlein & Gwinner, 2006), nestlings in territories within shrike territories were substantially lighter (by 13 % or more) than those well away from shrikes. This

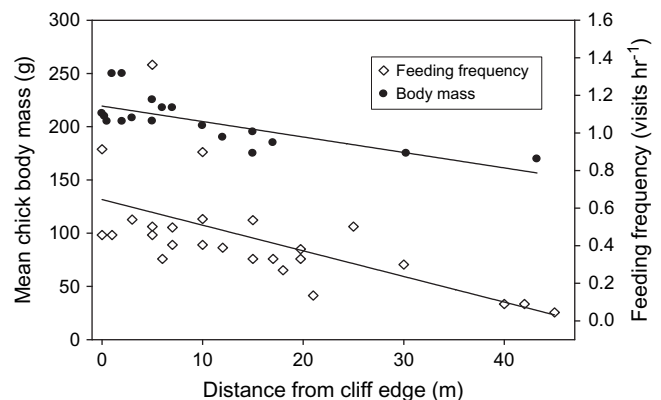


Fig. 8. Effect of distance to cliff edge on mean chick mass and rate of parental feeding visits by Inca terns (*Larosterna inca*) in Peru. Parents are at considerable risk of predation by peregrine falcons (*Falco peregrinus*) if they nest inland away from the cliff edge. Parents visited less often, and chicks fledged lighter, when nests were in riskier locations. Body mass was calculated over broods of (usually) two chicks at 25–30 days of age. Both least-squares regression lines are significant at $P < 0.001$. Data from Velando & Márquez (2002).

effect was due mainly to less time spent foraging by the parents. Finally, coastal-nesting tree swallows (*Tachycineta bicolor*) avoided feeding their young when gulls were roosting directly on their nest boxes (Wheelwright & Dorsey, 1991). The nestlings suffered a short-term loss in body mass as a result, but the parents were able to compensate for this loss such that the young suffered no long-term loss of mass (but see Mangel & Munch, 2005). This result may reflect the fact that parental swallows experience little risk from gulls away from nest boxes.

Most of the above cases deal with predators that pose a greater threat to adults than to nestlings. To what degree should a parent provision young when only the nest itself is at risk to predation? If parental activity attracts nest predators, then parents may have little choice but to curtail feeding under a higher predation risk (Eggers *et al.*, 2005; Fontaine & Martin, 2006b; Peluc *et al.*, 2008; but see Gardner, 2007). The qualitative effect would be similar to that observed when parents themselves are at risk. There are, however, ways that parents might avoid such costs. For instance, they might deliver larger loads of food to the nest on each visit (Martin *et al.*, 2000a; Eggers *et al.*, 2008). Keeping a sentinel on watch for nest predators is also an option; this may happen with male stonechats (Scheuerlein & Gwinner, 2006) and some cooperative breeders (see Bednekoff, Bowman & Woolfenden, 2008; Hollén, Bell & Radford, 2008). Auditory warning and all-clear systems may also help reduce the costs of dealing with a chronic risk to nests (see Section IV.1.b). However, if nest predators detect nests mainly by the noise generated by nestlings, then perhaps the best option is to keep the young as well fed (and unreactive) as possible (see also Grodzinski *et al.*, 2008).

(4) Intraspecific brood parasitism

It has long been suggested that intraspecific brood parasitism (IBP) represents a form of bet hedging against nest predation or reproductive failure in general (see Pöysä & Pesonen, 2007). Selection might favour such “risk-spreading” behaviour in the face of nest predation, even if overall mean fitness does not increase as a result (Gillespie, 1977); put more simply, a bird might benefit from not putting all of its eggs in a single, vulnerable basket (its own nest). Bulmer (1984) countered this simple idea, showing that selection for a reduction in fitness variation is likely to be fairly weak. Explanations of IBP thus turned to factors such as nest-site limitation, an inability to obtain a mate, *etc.* (e.g. Sandell & Diemer, 1999). A comparative analysis also suggested that IBP is associated with “fast” life histories (Arnold & Owens, 2002). IBP has been observed in most major avian orders, and appears especially prevalent in ducks, grebes, and galliforms, with a more limited frequency in passerines (Yom-Tov, 2001; Arnold & Owens, 2002).

That IBP acts as a form of risk-spreading has fallen out of favour, but a recent model by Pöysä & Pesonen (2007) shows that, as an anti-predation strategy, IBP can invade a population of non-parasites. The key assumption here is that a parasitic female has some knowledge about the predation risk experienced by conspecific nests. There is

little information on such matters, but Pöysä (1999, 2006) showed that common goldeneyes (probably *via* prospecting trips) preferentially parasitize conspecific nests with the lowest predation risk. Parasitic cliff swallows (*Hirundo pyrrhonota*) also seem to know which nests are most likely to produce offspring (perhaps reflecting ectoparasite infestation rather than predation *per se*; Brown & Brown, 1991). The model of Pöysä & Pesonen (2007) is not entirely a risk-spreading model, as the ability to assess nest vulnerability increases mean fitness in addition to spreading risk, but not putting all of one’s eggs in a single basket can clearly be a successful strategy. Another recent model suggests that IBP can be favoured under a scenario of partial nest predation *via* risk dilution in enlarged clutches (Roy Nielsen, Parker & Gates, 2008). An empirical result of relevance here is the observation by McRae (1997) that IBP increased markedly in moorhens (*Gallinula chloropus*) during periods of high nest predation by rats. This increase in IBP occurred prior to the production of a clutch for personal incubation (no female moorhens were exclusively parasitic), and thus was not simply a response to a given bird’s loss of a nest. There is obviously much work to be done on flexible IBP under the risk of nest predation, but the above studies suggest that such work will be worthwhile.

VI. SINGING AND THE RISK OF PREDATION

Singing is a prominent feature of the breeding season, especially in male passerines (Catchpole & Slater, 1995). Singing is clearly directed towards mate attraction and territory defence, but such noise production could easily attract the attention of predators (Zuk & Kolluru, 1998). This implies that the risk of predation could influence the way birds sing, although this possibility largely has been ignored (see Zuk & Kolluru, 1998). However, a recent comparative study by Møller, Nelson & Garamszeg (2006) provides a rare treatment of the subject, with clear implications for an ecological-time perspective on singing. For many species of European passerines, they related a measure of exposure while singing (an index of singing perch height) to a given species’ prevalence in the diet of sparrowhawks during the breeding season, and found a positive relationship, suggesting that singing is indeed dangerous. However, their analysis suggests that song features *per se* are not clearly related to predation risk. Further work (Møller, Nelson & Garamszeg, 2008) suggests that species singing from exposed perches accept relatively less risk during predator approaches than do species singing from more concealed perches.

The potential danger in singing (and other breeding vocalizations) has also been demonstrated under field conditions. For instance, a playback experiment showed that brown skuas (*Catharacta antarctica*) are attracted to the vocalizations of breeding blue petrels (*Halobaena caerulea*), which were their main prey at the study site (Mougeot & Bretagnolle, 2000). Group-chorusing in black-breasted wood-quails (*Odontophorus leucolaemus*) attracts several types of predators, as Hale (2004) discovered during a study designed

to trap and survey this species. Related studies on non-sexual vocalizations provide additional evidence for predator attraction. For instance, the mobbing calls of pied flycatchers can attract martens to nests, even though tapes were played during the day and the martens are active at night (Krama & Krams, 2004). The longer-range contact calls of crested tits (*Lophophanes cristatus*) are known to attract *Accipiter* hawks (Krams, 2001a), although this study was done when there were many migratory hawks in the study area.

(1) Flexible singing

The above observations suggest that singing in birds should be responsive to the local risk of predation, although there are few relevant studies. However, northern cardinals (*Cardinalis cardinalis*) tend to sing from relatively concealed perches when close to (within 100 m) the nests of Cooper's hawks (*A. cooperii*; Duncan & Bednekoff, 2006). Similarly, during the dawn chorus in the early spring, male blue tits tend to sing from the early-leafing trees (Parker & Tillin, 2006). For a somewhat contradictory result, Krams (2001b) suggested that chaffinches (*Fringilla coelebs*) prefer relatively exposed perches in the forest understorey under a higher risk of predation, possibly for better predator detection. Cresswell (1994b) observed that skylarks (*Alauda arvensis*) use in-flight songs as a sort of pursuit-deterrence signal, but this is probably unusual among passerines.

An important issue in the choice of singing perches is the extent to which exposed perches are risky places. The results of Møller *et al.* (2006, 2008) suggest that exposed singing tends to be more risky. However, in a study on hunting *Accipiter* hawks, Roth *et al.* (2006) observed that wintering birds (mainly passerines) attacked on exposed perches almost always escaped. Thus, it is not necessarily the case that birds singing in exposed locations are particularly vulnerable to predation. A key point here is how much singing interferes with the ability to detect predators (see also Cowlshaw *et al.*, 2004). If singing detracts from anti-predator vigilance, then singing from exposed perches might be dangerous; if not, then exposed singing may be relatively safe. It is impossible at present to know where a given species falls into these various categories of singing risk.

It seems likely that predation risk will influence the way birds choose to sing. Various aspects of the use of syllables or vocal modulations could be predation-risk dependent, as might be the structure of bouts of singing. However, Duncan & Bednekoff (2006) observed no change in call rate when cardinals sang from points near hawk nests. On the other hand, blue petrels respond to playbacks of the calls of their skua predators with a 50 % reduction in calling (Mougeot & Bretagnolle, 2000). Some non-singing studies are also relevant. Crested tits tend to use softer contact calls when feeding away from protective cover (Krama, Krams & Igaune, 2008). Searcy & Nowicki (2006) provide a relevant but difficult-to-interpret result on vocalizations in song sparrows. These sparrows have a soft and loud version of aggressive vocalizations. Searcy & Nowicki (2006) formed the reasonable hypothesis that soft vocalizations should be

used during aggressive encounters that occur in potentially dangerous situations. However they found that loud vocalizations were used more in the presence of playbacks of song sparrow alarm calls than in the latter's absence. Perhaps the results would have been different if a predator had actually been present.

Changes in the way male birds sing under the risk of predation could influence their ability to attract mates. That the characteristics of songs have a major impact on mate choice is a long-established fact in avian biology (Catchpole & Slater, 1995; Gil & Gahr, 2002). Hence if males do not sing as loudly in risky situations, then perhaps they will suffer in attracting mates (or defending a territory). Female birds may also be more reluctant to approach males singing in relatively dangerous places, as has been seen regarding male displays in other taxa (Warner & Dill, 2000; Hedrick & Dill, 1993). Alternatively, Møller *et al.* (2006) suggested that a male might advertise its quality by singing in a dangerous location (e.g. an exposed perch). Such males might enjoy better body condition that allows them to escape attack more readily. Body condition may affect song output in passerines (Thomas, 2002; Thomas & Cuthill, 2002), and it ought to be fairly easy to test the idea that body condition is reflected in risk-taking by singing males.

So far, I have considered risk to be that experienced by the singer. However, and perhaps surprisingly, the nest-predator removal study of Fontaine & Martin (2006a) found that males of several species increased their singing rates in the predator-removal areas. Such an effect might conceivably be in direct response to the lowered risk itself, but the relationship between singing and nest predation is not obvious. In fact, one might expect a lowered rate of singing by males under the watchman's song hypothesis (Wickler, 1985), since a reduced risk of nest predation would require less "all-clear" singing by males (see Section IV.1.b above). It is more likely that this increased singing stems from some indirect effect of predator removal, such an increase in territory quality or altered competitive interactions with conspecifics and heterospecifics (Fontaine & Martin, 2006a).

(2) The dawn chorus

Predation risk has barely been mentioned in studies of the dawn chorus, despite the fact that singing loudly in the dim, pre-dawn light seems potentially dangerous. The dawn chorus is a prominent feature of the avian breeding season, and it has received much attention over the years. Among the most popular and viable explanations for the dawn chorus is that the many benefits of singing can take place at a time when other important activities are not feasible, such as foraging (Kacelnik & Krebs, 1983; see also Berg, Brumfield & Apanius, 2006). Singing during the dawn chorus may be directed towards other males (e.g. Liu & Kroodsma, 2007) and/or towards potential mates (e.g. Mace, 1987; Dalziell & Cockburn, 2007). A few studies also suggest that earlier-singing males are higher ranking or those of generally higher quality (e.g. Otter, Chruszcz & Ratcliffe, 1997; Poesel *et al.*, 2006). Whatever its function, pre-dawn singing could be dangerous, especially since owls,

with their superior hearing and vision, might still be actively hunting.

Several aspects of the dawn chorus might thus be sensitive to the risk of predation, but I know of no studies that have addressed predation on dawn-singing birds. There are nevertheless a few relevant observations. First, male blue tits tend to sing from the most visually obstructive trees during the dawn chorus (Parker & Tillin, 2006). This is consistent with predator avoidance, but could also reflect a thermally advantageous environment. Another relevant observation is that the earliest-singing species are those with larger eyes, perhaps better adapted to low-light conditions (Thomas *et al.*, 2002; Berg *et al.*, 2006). This observation is consistent with the idea that singing can begin earlier if predators still can be detected. It is also likely that a dilution effect occurs when many males sing at once (see also Møller, 1992). Further studies here are clearly needed.

VII. DYNAMICS OF LEKKING

The idea that danger imposed by predators can promote the evolution of leks is an old one in avian biology (Lack, 1968). Birds in groups are more difficult to approach and capture (Cresswell, 1994a; Roth & Lima, 2003; Roth *et al.*, 2006), and lekking males should enjoy similar benefits. A review by Höglund and Alatalo (1995) concluded that predation does not generally drive the formation of leks in birds. However, this conclusion does not rule out a role for predation risk as a major ecological-time determinant of lekking behaviour.

Many of the relevant papers here are theoretical in nature rather than empirical. Boyko, Gibson & Lucas (2004) present a highly relevant model focused explicitly on flexible lekking under the risk of predation. Their model, based on group leks, is a stochastic dynamic game among males of differing ranks and mating prospects. The main trade-offs are between personal survival and the benefits of mating (see also Kålås, Peder, & Sæther, 1995). The model makes predictions about the temporal trends in lekking over a day, and which males are most likely to be at the lek. A prominent and supported prediction is that leks should be smaller and of shorter duration on windy days, since eagles are more active under such conditions. Boyko *et al.* (2004) did not provide detailed support for key assumptions regarding predation risk (a common problem; Lima, 2002), but their results suggest that predator avoidance is an important aspect of lek dynamics.

Isvaran & St. Mary (2003) present a stochastic dynamic model that highlights the factors that might promote clustering of males (this model is based on an ungulate system, but is relevant here). They found that an accelerating preference for clustered males by females is the major factor promoting classic lekking. Changes in predation alone do not have much effect on male clustering (lek formation), but predation and female bias for clustering can interact strongly to produce standard leks. Predator avoidance itself might be a reason for females to prefer visiting grouped males in some circumstances, so predation could be doubly important. This

model suggests that in some systems lekking might be highly dynamic with changes in predation risk: this appears to be the case in Uganda kob (*Kobus kob thomasi*). Regarding the choices actually made by females at a lek, Hamilton, Haesler & Taborsky (2005) present a model which suggests that lower quality males may enjoy some mating success if the enemies (broadly defined) of females tend to associate with the high-quality males. This model probably does not apply to standard avian leks (since predators cannot readily associate with specific males), but could conceivably apply to males in more dispersed “exploded” leks (Höglund & Alatalo, 1995). Once again, however, this model stresses that lekking dynamics should be sensitive to changes in risk over ecological time.

An early empirical study on lekking in the cock-of-the-rock (*Rupicola rupicola*) is a unique example of the sort of empirical studies that are needed here. Trail (1987) studied a stable cock-of-the-rock lek in an area of South America with an intact predator fauna. The lek was attacked fairly frequently by several different raptors. These raptor attacks were not very effective, since the males in the lek clearly enjoyed a sort of vigilance-based early-warning system. Surprisingly, the more dangerous predator was a snake that the males seemed unable to detect easily. The relatively frequent attacks might suggest that leks attract predators, but overall, the lekking males were fairly safe. The key (un-made) comparison would be the safety level associated with displaying alone or in small groups. It might also be the case that raptors do not tend to focus on such prey hotspots (Roth & Lima, 2007). Additional work on this species suggests that the use of light by displaying males enhances their short-range detectability (mainly to females) without much increase in long-range detectability to predators (Endler & Théry, 1996; see also Heindl & Winkler, 2003).

Studies of North American grouse suggest that predators play an important role in lekking. In addition to the game theoretical model mentioned above (Boyko *et al.*, 2004), Aspbury & Gibson, (2004) show that sage grouse (*Centrocercus urophasianus*) choose lek sites located in low spots surrounded by nearby low hills that enhance short-range visibility (< 500 m) but prevent easy long-range monitoring by eagles. Lekking sage grouse are very sensitive to the presence of golden eagles (*Aquila chrysaetos*), and will flush to safety when eagles are detected even at a distance (Hartzler, 1974). Deutsch & Weeks (1992) argue similarly that lekking ungulates prefer high-visibility leks. Gibson, Aspbury & McDaniel (2002) suggest that greater prairie chickens (*Tympanuchus cupido*) sometimes join leks of other grouse species to gain the social anti-predator advantages mentioned above, perhaps without suffering a great disadvantage from being in a heterospecific lek. If this is the case, then changes in such mixed-species lekking should track changes in predation risk.

VIII. ADJUSTMENTS IN BODY MASS

Body mass changes over the breeding cycle are common in many species of birds (see Freed 1981), and some aspects of

these changes might be linked to changes in local predation risk. Historically, however, most explanations of this effect have not involved predation. Freed (1981) formalized the idea that the post-incubation decrease in body mass seen in birds is an adaptive strategy to reduce wing-loading and thus increase the efficiency of flight in anticipation of the demands of feeding nestlings. This and related work has spawned scores of papers, often with contradictory results and conclusions. For instance, some parental birds (usually females) did not lose body mass early in the nestling stage when provided with supplemental food (e.g. Cucco & Malacarne, 1997; Holt *et al.*, 2002). This result suggests that mass loss may reflect the energetic stress of feeding offspring rather than a strategic drop in body mass to improve flight performance. A larger number of studies show that the body mass loss occurs despite the availability of supplemental food (e.g. Merkle & Barclay, 1996; Slagsvold & Johansen, 1998; Cavitt & Thompson, 1997), which suggests a strategic loss in mass.

A post-incubation reduction in body mass might reflect an adaptive response to the risk of predation (Lima, 1986). Several studies now show that a bird's escape performance can be compromised by extra body mass (Pravosudov & Grubb, 1997; Lind, Jacobsson & Kullberg, in press; see also Veasey, Metcalfe & Houston, 1998; Veasey, Houston & Metcalfe, 2000). Such performance effects are most noticeable when birds fly with masses typical of migration (Kullberg, 2000), incubation (Kullberg, Houston & Metcalfe 2002*b*) or while carrying a developing egg (Kullberg, Houston & Metcalfe, 2002*a*, Kullberg *et al.*, 2005), but may also occur with lesser weight gains (e.g. Witter, Cuthill & Bonser, 1994). There are no studies which directly link such mass-driven changes in flight performance to predation (which would be a difficult task), but Slagsvold & Dale (1996) showed that a slight change in flight performance in breeding pied flycatchers (as a result of feather clipping) can lead to a substantial increase in predation. It is thus conceivable that the post-incubation loss of mass is linked, in ecological time, to the local risk of predation experienced by a given bird (but see also Barta *et al.*, 2002). For instance, maintaining some extra mass might be beneficial for purposes of re-nesting, but only if the local risk is not too high (see also Houston *et al.*, 2007). Such effects might even link variation in predation risk to that in clutch size (see also Veasey, Houston & Metcalfe, 2001). These scenarios ought to be testable in situations taking advantage of natural variation in predation risk relative to hawk nest proximity, etc. Perhaps work incorporating a predation-risk perspective will shed some light on the above-mentioned contradictions in body mass changes in response to food supplementation.

IX. CONCLUSIONS

(1) A growing body of work shows that breeding birds have a significant capacity to assess and respond adaptively in ecological time to changes in the risk of predation, both to themselves and their offspring. Published work covers

a variety of behavioural and reproductive decision-making contexts, and complements the large body of comparative work on avian breeding biology.

(2) Work on avian nesting biology has long been focused on nest predation, since it is the most important source of reproductive failure. Accordingly, most work on anti-predator flexibility in breeding birds is also focused on nest predation. Nesting in a new location in response to nest loss appears to be widespread at both large and small spatial scales. One can also imagine differing degrees of sophistication in nest placement strategies regarding the risk of nest predation, but the degree to which birds avoid areas with a high risk of nest predation is unclear.

(3) Outside of nest predation, avian reproduction and breeding behaviour have received relatively little attention from the perspective of flexibility in the face of changing predation risk. This is true of almost all of the topics considered herein, such the nature of breeding-season sociality, singing, body mass dynamics, and lekking dynamics, as well as life-history characteristics such as clutch size or egg volume. The available studies, however, do suggest that anti-predator flexibility exists in a variety of contexts.

(4) The nature of the information available to breeding birds about the risk of predation is particularly important here, since such information will ultimately determine the nature of the behavioural or reproductive flexibility that one might expect to observe. There are potentially many sources of such information, but little hard evidence. This is particularly true of information about nest predators.

(5) Research on almost all topics covered herein is in its infancy, and thus all areas need more empirical as well as theoretical attention. There is also a need for much more experimental work. Work to date strongly suggests that continued efforts will be rewarded with new insights into the biology of breeding birds.

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