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Review

Non-lethal effects of predation in birds

WILL CRESSWELL*
Bute Building, School of Biology, University of St. Andrews, Fife, KY16 9TS, UK

Predators can affect individual fitness and population and community processes through lethal effects (direct consumption or 'density' effects), where prey is consumed, or through non-lethal effects (trait-mediated effects or interactions), where behavioural compensation to predation risk occurs, such as animals avoiding areas of high predation risk. Studies of invertebrates, fish and amphibians have shown that non-lethal effects may be larger than lethal effects in determining the behaviour, condition, density and distribution of animals over a range of trophic levels. Although non-lethal effects have been well described in the behavioural ecology of birds (and also mammals) within the context of anti-predation behaviour, their role relative to lethal effects is probably underestimated. Birds show many behavioural and physiological changes to reduce direct mortality from predation and these are likely to have negative effects on other aspects of their fitness and population dynamics, as well as affecting the ecology of their own prey and their predators. As a consequence, the effects of predation in birds are best measured by trade-offs between maximizing instantaneous survival in the presence of predators and acquiring or maintaining resources for long-term survival or reproduction. Because avoiding predation imposes foraging costs, and foraging behaviour is relatively easy to measure in birds, the foraging–predation risk trade-off is probably an effective framework for understanding the importance of non-lethal effects, and so the population and community effects of predation risk in birds and other animals. Using a trade-off approach allows us to predict better how changes in predator density will impact on population and community dynamics, and how animals perceive and respond to predation risk, when non-lethal effects decouple the relationship between predator density and direct mortality rate. The trade-off approach also allows us to identify where predation risk is structuring communities because of avoidance of predators, even when this results in no observable direct mortality rate.

Keywords: indirect effects, predation risk, starvation risk, trait-mediated effects, trait-mediated interactions.

Prey population density can be reduced both by direct consumption by predators and by non-lethal effects, as predators 'scare' prey away (Abrams 1984). Such behavioural responses to variable predation risk have been identified in many studies (Lima & Dill 1990, Lima 1998a): animals frequently act in ways to avoid predators, or to avoid capture when a predator is present, so that their immediate survival is increased. Reducing immediate predation risk, however, usually leads to foraging in areas or in ways that reduce longer term survival or overall resource levels available for reproduction. As a result of this trade-off, predation risk may then result in non-lethal fitness consequences, such as reduced foraging rates, slower growth rates and lower reproductive rates. It is becoming increasingly clear that the non-lethal consequences of predation risk, whether through morphological or behavioural compensation, are very important in determining population and community dynamics in a variety of taxa (Agrawal 2001). Although the potential ecological consequences of non-lethal effects have already been well reviewed (e.g. Lima 1998b), we still lack a clear appreciation of their relative importance compared to direct mortality effects in terrestrial vertebrate systems. Birds have potentially some of the most complicated anti-predation and

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*Email: wrlc@st-and.ac.uk

predation behaviours (Caro 2005), and therefore it might be expected that the non-lethal effects of predation risk should dominate their evolutionary, population and community ecology. If non-lethal effects are important, they cannot be ignored because they will, for example, result in a lack of a linear relationship between death rate or response of prey with predator number, so leading to many important consequences for our understanding of population dynamics, our management of populations and use of biological control (Abrams 1993). This review presents a synthesis of some of the evidence to show the relative importance of the non-lethal effects of predation (trait-mediated effects or interactions) in avian systems. Very good evidence also comes from mammalian systems that share many of birds' complex range of anti-predation and predation behaviours (Caro 2005). Having acknowledged the importance of non-lethal effects, the best framework in which to measure the effects of predation risk is then a trade-off, because although reducing predation risk through behavioural and physiological means may increase survival in the short term, reducing predation risk will often result in a decrease in resources available for survival in the long term, or for fecundity, reducing overall fitness. I then explore the main consequences of acknowledging the importance of non-lethal effect for studies of avian predation; in particular, how prey animals' perception of predation risk and their range of options in avoiding predators structures population and community dynamics, rather than simply per capita mortality rate.

SYNTHESIS

Definitions of non-lethal effects

The terminology of non-lethal and direct mortality effects has been most clearly stated to date by Luttbeg and Kerby (2005). 'Trait-mediated effects' (or – synonymously – 'trait-mediated interactions') occur where predators affect individual prey fitness through non-lethal (or non-consumptive) effects on traits, such as individuals leaving a profitable feeding area because of predation risk. The predator directly influences the fitness of its prey because the prey's options are constrained and the behavioural response may be costly. The predator also indirectly alters the constraints operating on other species (e.g. competitors or prey of the focal prey species), for example through a reduction in the density of the prey in the area the prey now avoids, and through an increase in the density of the prey in the area the prey now uses. Trait-mediated effects contrast with 'density effects', where predators reduce prey density through killing prey. The predator has a direct mortality effect on the prey, a direct effect on the characteristics of the area through a reduction in the prey's density and an indirect effect on the resource density of the prey it has consumed. In essence, reduction in prey density, whether through non-lethal effects or direct consumption, changes the ecological constraints of an area through reduction in intra- and interspecific competition at the prey's own trophic level. Reduction in prey density also changes competition and predation at both lower and higher trophic levels than the prey, because any prey will itself eat other animals or plants, and be prey for other predators. Where an effect involves three trophic levels, for example the effect of a predator on the resources of its prey, this has been called a 'trait-mediated indirect interaction' (Preisser *et al.* 2005). In an effort to keep the terminology simple, and because trait-mediated effects frequently involve changes in prey density, I refer to 'trait-mediated effects' as non-lethal effects, and 'density effects' as lethal effects throughout, as per some earlier literature (e.g. Lima 1998b).

The relative importance of non-lethal and lethal effects

Indirect non-lethal effects have been identified as important in a large number of studies (Werner & Peacor 2003), and early ideas of the importance of non-lethal effects demonstrated how refuge behaviour of prey can stabilize predator–prey population dynamics (Sih 1987, 1997). Recent reviews have suggested that the non-lethal effects of predation may be as, or more, important than its lethal effects. Preisser *et al.* (2005) reviewed 166 estimates of effect size from 49 published studies and found that the strength of direct (i.e. at one trophic level) lethal and non-lethal effects are similar, but that indirect non-lethal effects (i.e. including effects at other trophic levels) were 85% of all effects (i.e. lethal and non-lethal). Non-lethal effects were found to be largest in aquatic systems (including several fish and amphibian studies), but terrestrial studies to date have largely been limited to invertebrates. More recent studies have continued to confirm the relative importance of non-lethal effects, demonstrating, for example, that non-lethal effects of predators may reduce energy transfer in food chains and so limit their length (Trussell *et al.* 2006), and the ecological conditions under which they become more important (Werner & Peacor 2006). Theoretical studies have also predicted the relative importance of non-lethal effects (although see Persson & de Roos 2003, Schmidt 2004, Krivan & Sirot 2004, Krivan & Schmitz 2004, Peacor & Werner 2004a, 2004b, Holker & Mehner 2005).

Most examples of strong non-lethal effects come from invertebrates and particularly from aquatic pond systems, because the scale for multi-trophic observation and manipulation is tractable, and because the lethal effects of predators can be limited experimentally. For example, Nelson *et al.* (2004) surgically shortened the proboscis of damsel bugs, so preventing them from consuming pea aphids but not from disturbing them: the study showed that non-lethal effects alone can reduce aphid population growth (by 30% in this case). Other experimental demonstrations of non-lethal effects use predator exclusion experiments; for example, caging aquatic predators such as dragonfly larvae within ponds so that they are present but cannot feed on prey outside their cages (e.g. Peacor & Werner 2001).

A few studies have specifically attempted to partition non-lethal and lethal effects in terrestrial vertebrates, usually using exclosures to exclude predators and working under the assumption that the prey species will still behave as if under predation risk, even though predation mortality has effectively been removed. These studies have mainly been carried out in mammals, probably because such exclosure experiments are more tractable. All such studies have identified non-lethal effects of predation risk, such as changes in body condition or growth rates, for example in Snowshoe Hares *Lepus americanus* (Hik 1995), Arctic Ground Squirrels *Spermophilus parryii* (Karels *et al.* 2000) and House Mice *Mus musculus* (Arthur *et al.* 2004). Other studies have observed changes in body condition and reproductive success with changes in predator density, by experimentally reducing predator density, for example reducing Red Fox *Vulpes vulpes* density and observing effects on Native Bush Rats *Rattus fuscipes* (Banks *et al.* 1999), observing natural variation in relative predator density, for example during population changes in Wildebeest *Connochaetes taurinus* (Sinclair & Arcese 1995) and across populations of Elk *Cervus elaphus* that differed in relative abundance of Wolves *Canis lupus* (Creel *et al.* 2007), or by experimentally increasing perceived predator density, for example nesting Common Buzzards *Buteo buteo* presented with models of Northern Goshawks *Accipiter gentilis* (Krűger 2002).

Responses to predation risk in birds as non-lethal effects

Birds as a taxon are perhaps particularly likely to show non-lethal responses to predation risk. Birds are characterized in most cases by their ability to fly, their relatively large size, their well-developed cognitive abilities and their laying of eggs that require incubation. These characteristics all probably act together so that anti-predation behaviours have a substantial impact on fitness, and on population and community dynamics. Although non-lethal effects such as avoidance (and so patch choice and distribution), grouping, vigilance, escape responses, alarm calls, and defences against predators have been described in the context of anti-predation behaviours, their consequences for overall fitness and population and community dynamics have often been ignored in studies of birds (Lima & Dill 1990, Lima 1998a). I illustrate this with three examples that show how well described anti-predation behaviours can lead to less well described non-lethal effects.

Firstly, because birds can fly, they are constrained in carrying fat reserves because of the effects additional mass has on take-off speeds and flight acceleration (Witter & Cuthill 1993). For example, fatter Blackcaps *Sylvia atricapilla* and European Robins *Erithacus rubecula* show substantial reductions in escape flight performance when presented with models of attacking predators (Kullberg *et al.* 1996, Lind *et al.* 1999). This creates a conflict with minimizing starvation risk because birds deal with unpredictability of foraging opportunities (i.e. during the winter when the foraging environment is poorer) by increasing fat reserves which increase mass and so predation risk (Cresswell 1998, MacLeod *et al.* 2005). Non-lethal consequences for fitness and population dynamics may then arise because of lower survival and lower reproductive output. For example, birds in poor foraging environments that cannot afford to pay the costs of increased fat reserves, because they cannot avoid predators, are more likely to have declining populations both within and across most species examined (MacLeod *et al.* 2006, 2007). Non-lethal consequences for community dynamics then may also arise because the prey are restricted to safer areas, which has a knock-on effect on the distribution and dynamics of their predators (bottom-up control) and their own prey (top-down control).

Secondly, because birds are relatively large, mobile and behaviourally sophisticated, they can either avoid predators by movement, or by reducing their profitability so that predators hunt alternative prey. Birds operate over a large spatial scale, and can avoid predators through movements such as migration (for example, sandpipers avoiding migration stopovers where there are Peregrines *Falco peregrinus* (Lank *et al.* 2003)). They can also, conversely, use otherwise high predation risk areas (Lima 1992) such as open areas with no safe cover because cohesive group and escape flight behaviour reduces predation risk. For example, Common Redshanks *Tringa totanus* have lower risk of capture when attacked in flocks, probably because of the confusion effect (Cresswell 1994b). Alternatively, high risk enclosed areas can be used, such as predator-concealing dense forest, where mixed flocking, vigilance and sentinel behaviour reduces predation risk. For example, vulnerable ground-feeding bird species may be able to utilize more predator concealing habitats if they associate with more arboreal feeding 'sentry' species (Thiollay 1999). Non-lethal consequences for fitness, population and community dynamics might then arise because social behaviour in one prey species provides the prey species with a greater availability of relatively safe foraging opportunities, allowing use of a greater range of habitats and ability to forage on different prey, with knock-on effects on predators then obliged to hunt an alternative, more vulnerable prey species.

Thirdly, because birds must incubate their eggs and brood their pre-fledging young, they must also invest heavily in behaviours that allow them to nest secure from predators. For example, hole-nesting species must either create or acquire, and often defend, nest holes that are usually in short supply (Newton 1994), and minimize the risk of discovery of their nests from predators by choosing hidden or relatively inaccessible nest sites (Martin & Roper 1988). Open nesting species often must defend their nest, for example, through fighting off predators as in kingbirds *Tyrannus* (Blancher & Robertson 1982), or through distraction of predators near the nest as in shorebirds (Byrkjedal 1987). The non-lethal consequences of these behaviours for fitness and population dynamics might be through restriction of foraging opportunities, and reduction in parental visits to the nest with a consequent reduction in feeding rates to chicks. Further non-lethal effects arise because of possible effects on clutch size and other life history aspects such as breeding system, as when the need for two parents for nest defence selects for monogamy (Larsen 1991), or for long incubation periods reducing activity at the nest (Cresswell *et al.* 2003), which may then further affect survival rates. Again, there might be consequences for community dynamics because of changes in the distribution of the species during breeding, and the effects on their predators and prey.

Ecological consequences of non-lethal effects in birds and mammals

Several studies have described the importance of non-lethal effects of predation risk in shaping community dynamics and the evolution of birds and mammals. Brown *et al.* (1999) formalized the term the 'ecology of fear' to describe how in mammalian systems, where behaviourally complex predators hunt behaviourally complex prey, populations may be limited by the 'fear' of predation resulting in loss of feeding opportunities. Lima (2002) reviewed how non-lethal effects of predators, and the reverse, how these non-lethal effects on behaviour of the prey lead to the predator's own behavioural changes (i.e. predator–prey 'games'), are crucial in understanding animal movement and habitat choice.

Key to understanding the ecological consequences of non-lethal effects is considering how prey avoid predators. Perhaps one of the most common ecological consequences of non-lethal effects in birds is the change in foraging opportunities and competition at different trophic levels, in both time and space, because prey avoid hunting predators. This could impose increased competition on all prey individuals as they exploit the reduced opportunities for foraging where and when the predator is not present; for example, Elk *Cervus elaphus* have lower diet quality because of habitat shifts in the presence of Wolves *Canis lupus* (Hernandez & Laundre 2005). The most evident fitness consequences of predation risk will then be increased unpredictability of foraging with subsequent effects on starvation risk. An example of this is the interrupted-foraging response, where birds increase fat reserves as predation risk increases because avoiding predators reduces time or space available to forage (Houston & McNamara 1993, MacLeod *et al.* 2007). Avoidance should also then have effects on fitness, for example, Pied Flycatchers *Ficedula hypoleuca* that have to nest close to a Eurasian Sparrowhawk *Accipiter nisus* pay a fitness cost in terms of reduced clutch sizes (Thomson *et al.* 2006), possibly because of diversion of resources from reproduction to anti-predation behaviour. Conversely, predation risk could lead to reduction in competition and increased predictability of foraging opportunities for non-prey (because prey avoid areas where non-prey can remain), or even for the prey themselves if starvation risk is so high that predation risk has to be largely ignored. For example, Redshanks can feed relatively well in dangerous saltmarsh areas when they are starving because normally such areas are avoided by the local population, and hence food supplies have not been depleted (Yasué 2005, Cresswell & Whitfield 2008).

Non-lethal effects on community dynamics in birds and mammals have most often been empirically described as part of the concept of intra-guild predation. Here, one or more species acts as both predator and competitor with other species at the same or similar trophic level, and so distribution and predation rates are affected as predators avoid each other (Polis *et al.* 1989, Fedriani *et al.* 2000). There are now many examples of how non-lethal effects structure raptor populations. For example, Tengmalm's Owls *Aegolius funereus* breed in sub-optimal habitats to avoid Ural Owls *Strix uralensis* (Hakkarainen & Korpimaki 1996), and Black Kite *Milvus migrans* distribution is determined by avoidance of Eurasian Eagle Owls *Bubo bubo* (Sergio *et al.* 2003). Similar examples exist for mammalian carnivore populations (Kelly *et al.* 1998, Arjo & Pletscher 1999, Palomares & Caro 1999, Durant 2000). Modifications of this principle, where prey associate with more vulnerable prey to avoid attack (e.g. Zebra *Equus burchelli* with Wildebeest, Sinclair 1985), or prey associate with heterospecifics better able to detect (e.g. gulls as sentinels for shorebirds, Thompson & Barnard 1983) or deter predators (e.g. nesting of geese with raptors, Quinn & Kokorev 2002), are probably common and affect fitness indirectly through changing predator and prey distribution, and inter- and intra-specific competition.

Community effects such as changes in spatial and temporal patterns of abundance in birds and mammals have been shown to result from avoidance of predators, for example farmland birds avoiding Common Kestrel *Falco tinnunculus* breeding sites (Suhonen *et al.* 1994), and Thirteen-lined Ground Squirrels *Spermophilus tridecemlineatus* choosing feeding habitats to avoid Red Fox urine and plastic models of owls (Thorson *et al.* 1998). Behavioural compensation in response to nest predation has also been widely documented, for example Black Kites changing nesting sites between years in response to nest predation (Forero *et al.* 1999), and increased dispersal distance in Tengmalm's Owls exposed to an American Mink *Mustela vison*, a potential nest predator (Hakkarainen *et al.* 2001). The outcome is potentially profound distribution effects such as many seabirds being restricted to predator-free islands (e.g. Anderson 1991). Studies of human disturbance to wildlife have also involved the widespread documentation of non-lethal effects that result in avoidance (Sutherland 1996, Gill *et al.* 2001), sometimes with profound cascading trophic effects. For example, increases in human visitors at a site reduced Cougar *Felis concolor* densities, which subsequently led to higher Mule Deer *Odocoileus hemionus* densities, higher browsing intensities and so reduced recruitment of riparian trees, increased bank erosion, and reductions in both terrestrial and aquatic species abundance (Ripple & Beschta 2006b).

Indirect non-lethal effects, i.e. those that impact across trophic levels, have been described in relatively few bird systems (e.g. see Mooney 2006), probably primarily because of the scale at which non-lethal effects can operate (Lima 1998b). However, any study that discusses 'top-down' or 'bottom-up' control (e.g. Meserve *et al.* 2003, Frederiksen *et al.* 2006), where predators control prey populations or vice versa, is likely to involve non-lethal effects. For example, Common Redshank mortality is under both top-down control, because birds move to less-profitable feeding areas to avoid Eurasian Sparrowhawk predation (Cresswell 1994a, Yasué *et al.* 2003), and bottom-up control, because an avoidance response by the Redshanks' own prey prevents them from grouping effectively to resist Sparrowhawk attack (Minderman *et al.* 2006). Other examples of non-lethal effects leading to trophic cascades are low rates of songbird nest predation when mice modify their nocturnal behaviour to avoid predation by owls (Schmidt 2006), habitat structure being determined by herbivore avoidance of Wolves in the Yellowstone ecosystem (Ripple & Beschta 2004, Creel *et al.* 2005, Ripple & Beschta 2006a), and community population dynamics being determined by rainfall influencing the anti-predation behaviour options of prey (Owen-Smith & Mills 2006). There are also several examples of the importance of cascading non-lethal effects in population regulation from studies of cycling populations (Krebs *et al.* 1995, Hik 1995, Norrdahl & Korpimaki 2000).

It is perhaps finally worth mentioning that parasitism provides a system in which there are lethal and non-lethal effects, and which has been widely studied in birds. Non-lethal effects have, however, been considered a fundamental part of the fitness, population and community effects of parasitism in birds unlike predation, where consideration of lethal effects has tended to dominate. For example, reproductive output, survival and occupation of breeding sites in Cliff Swallows *Petrochelidon pyrrhonota* is dependent on the number of ectoparasites (Brown & Brown 1986, Chapman & George 1991). Similarly, the non-lethal effects of parasites can lead to lower reproductive output in Red Grouse *Lagopus lagopus scoticus* (Hudson 1986), population cycling (Dobson & Hudson 1992, Redpath *et al.* 2006), and even increased susceptibility to predation (Hudson *et al.* 1992) by compromising a bird's ability to respond appropriately to predation risk. Red Grouse therefore provide an example of how the non-lethal effects of parasitism interact with the non-lethal effects of predation, where the effects of parasitism (i.e. on condition) can be viewed as an ecological constraint reducing a bird's ability to respond to predation risk. The effects of parasitism can also be considered one of the non-lethal effects of predators. Where predation risk is high, prey may become stressed with consequences to their immune function and their ability to deal with parasites and so fitness (e.g. Navarro *et al.* 2004). Parasitism studies in birds therefore may provide many good examples of how non-lethal effects can have profound ecological consequences, but with a key difference from the non-lethal effects of predation: although the effects of parasitism correlate positively with number of parasites, predation risk is not dependent necessarily on predator density, so requiring a more complicated approach to assess its effects.

Understanding non-lethal effects: the trade-off approach

Having established that non-lethal effects occur commonly, and that they are likely to be relatively important in avian systems, the next step is a framework that can measure the indirect effects of predation risk, rather than simply assuming that direct mortality reflects predation risk. It is clear from almost all studies that have examined non-lethal effects, that a single predator can influence the fitness of many individuals, even if few, if any, prey, are consumed (e.g. Trussell *et al.* 2004). Therefore, perhaps the most important characteristic of non-lethal effects is that they are not limited to the functional response of the predator: for example, a few Peregrines can cause a very large population of Western Sandpipers *Calidris mauri* to avoid an area even though the predators can only eat a small proportion of available prey (Ydenberg *et al.* 2002). Simplifications such as predation risk reflecting the ratio of prey standing stock to prey consumed by the predator (per-capita mortality rate), which are frequently used in theoretical models that explore predation risk, are therefore potentially unreliable (Abrams 1993, 1994). For example, although per-capita prey mortality induced by individual predators must decrease at high prey densities, non-lethal effects seem likely to continue to increase monotonically with predator numbers (e.g. Ydenberg *et al.* 2004). This lack of a linear relationship between non-lethal effects and lethal effects with predator numbers (Abrams 1993) means that the effects of predation cannot be assessed by simply measuring predator density, death rate or per-capita mortality risk: an alternative approach using trade-offs is required.

Engagement in anti-predator behaviours will often reduce the opportunity to engage in other activities. Although reducing predation risk through behavioural and physiological responses may increase survival in the short term, it may result in a decrease in resources available for survival or fecundity in the longer term. In other words, changes in predation risk, starvation risk and fecundity will not be independent of each other, and the appropriate framework in which to measure the effects of predation risk is via a trade-off. The costs and benefits of diverse anti-predation responses can then be measured by a common currency of changes in survival or reproductive output, or proxies such as food intake or body condition.

Measuring effects on fitness caused by anti-predation responses requires measures of reproductive output and a detailed knowledge of all aspects of the natural history of species in a system under consideration (Lind & Cresswell 2005, Ajie *et al.* 2007). Although studies that measure changes in reproductive success as a measure of fitness (or some proxy of changes in reproductive output such as abundance, controlling for habitat and distribution changes) due to changes in predator density, come close to this (e.g. Tharme *et al.* 2001), most studies cannot easily measure total fitness. However, the trade-off between allocating resources to anti-predation behaviour and reproductive output provides a framework in which to model the strength of predation risk and its effects on fitness, and the consequences of this for population dynamics (Abrams 1984, McNamara & Houston 1987, Abrams 1993). In essence, predation is a foraging cost, and foraging theory can be used to measure it quantitatively or qualitatively (Brown 1999, Brown & Kotler 2004), and foraging rates determine resources available for reproduction. Therefore, in many cases the foraging–predation risk trade-off (the relative investment in foraging versus anti-predation behaviour) can be used as the framework in which to measure non-lethal effects. Measuring actual intake rate relative to potential intake rate (i.e. when this is maximized by the animal) will allow predation risk to be quantified in terms of a foraging cost, even in a system where no predation mortality is evident (Lima 1986, Houston *et al.* 1993).

The foraging–predation risk trade-off allows us to understand population dynamics fully. For example, the population consequences of predation are best predicted by the availability of food, predator hunting behaviour and prey avoidance behaviour of risky areas in diverse animals such as Wildebeest (Sinclair & Arcese 1995) and Grey Partridges *Perdix perdix* (Watson *et al.* 2007). The foraging–predation risk trade-off can also allow us better to understand how non-lethal effects affect population processes such as compensatory mortality. When 'weak', poor condition individuals that 'would have died anyway' (e.g. from starvation), or animals that fail to breed are killed by predators, this may be interpreted as evidence for the relative unimportance of predation (Errington 1946). Yet, the foraging–predation risk trade-off framework allows us to understand condition-dependent mortality, which arises in cases where the cause of poor condition is the impact of predation risk on individuals' ability to feed or find refuge, not as compensatory, but as the end of a continuum of additive mortality caused by non-lethal effects on foraging rates (e.g. see Singer *et al.* 1997, Boyce *et al.* 1999, Tveraa *et al.* 2003).

Foraging–predation risk trade-off functions can be used successfully to explain diverse ecosystem processes (Bolker *et al.* 2003). The relative predation risk–foraging trade-off made by prey has a direct link with abundance at different trophic levels (Ovadia & Schmitz 2002). The relative importance of lethal and non-lethal effects, the direction and strength of indirect effects and their consequence for trophic cascades have been shown to be predictable from knowledge of habitat and resource use by prey with regard to a predators' presence, habitat use and hunting mode (Schmitz *et al.* 2004). It has also been empirically shown that the relative importance of non-lethal effects, and their magnitude and direction, depends on resource levels (Luttbeg *et al.* 2003, Bolnick & Preisser 2005): this can only arise if predation risk is related to starvation risk. The foraging–predation risk trade-off also provides a framework for understanding proximate mechanisms of non-lethal effects (Kavaliers & Choleris 2001) and how they arise as a consequence of behavioural syndromes (Sih *et al.* 2004). Theory (Abrams 1991) and meta-analyses (Bolnick & Preisser 2005) both also indicate that the effects of foraging–predation risk trade-offs in determining non-lethal effects are likely to be greatest in terrestrial systems involving mammals and birds because life histories are complex, and behaviours that provide complete protection from predation mortality when starvation risk is low are common.

PROSPECTUS

The most important consequence of non-lethal effects is that studies of the effects of predation risk must consider how resources have been diverted away from long-term survival or reproductive output in response to predation risk. In practical terms this means that any study that measures whether predators affect prey populations which does not directly measure a predator's effects on prey fitness, should measure how intake rates vary in the presence of predators. It should also measure how distribution reflects predation risk, rather than maximization of intake rate, as well as measuring direct mortality rate. In Common Redshanks, for example, evidence of the effects of predators determining their distribution in mild winters only comes from measurements of foraging rates that show Redshanks are far from optimizing intake rates in their choice of foraging habitat (Cresswell & Whitfield 2008). Appreciation of the importance of non-lethal effects should lead to a shift away from simply using predator density, death rate or per capita mortality rate as estimates of the effects of a predator, and a better understanding of how avoidance of predators may dominate many species' ecology. Some examples of important points to consider when studying predation in the light of non-lethal effects are outlined below.

How many prey predators directly kill may not indicate whether predators influence population dynamics

The hypothesis that predators are relatively important in bird population dynamics compared to other factors such as parasitism or abiotic factors is frequently tested in terms of the direct lethal effects of predation: by measuring the number of prey killed, or by comparing mortality due to predators to that from other sources (see studies reviewed in Newton 1998). Evidence from other taxa suggests that indirect effects may be as, or even more, important than lethal effects, yet few bird and mammal studies have acknowledged the role of non-lethal effects, let alone attempted to measure them (e.g. Hebblewhite *et al.* 2005, Gude *et al.* 2006). As a result, even studies that report large direct mortality may have underestimated the overall effects of predators, and studies that argue that predators do not contribute significantly to population dynamics, because there are no measurable direct effects, are likely to be fundamentally flawed.

In practical terms, the effects of predation can only be determined by considering both non-lethal and lethal effects, and future avian studies should not use low direct mortality rate as evidence to argue that predators do not contribute significantly to population dynamics. Experimental removals of predators and subsequent measurements of reproductive rates of prey can provide a valid assessment of the overall effects of predation (e.g. Marcstrom *et al.* 1988, Tapper *et al.* 1996), but they cannot distinguish between lethal and non-lethal effects. Appreciating that direct mortality does not indicate the overall effect of predation provides an insight for other applied situations. For example, anthropogenic situations that involve direct mortality as well as disturbance avoidance such as wind farms (Drewitt & Langston 2006) and hunting (Tamisier *et al.* 2003) cannot use evidence of low direct mortality alone as evidence of small effects on population dynamics.

Perceived predation risk is important rather than per capita risk of mortality

Available evidence suggests that an animal responds more to 'perceived' predation risk based on how local conditions affect capture probability on attack (e.g. Thorson *et al.* 1998, Orrock *et al.* 2004, and see Stankowich & Blumstein 2005 for a review) than to actual per-capita mortality rates. The mismatch between perceived and actual predation risk probably then arises because predators target individuals that they are most likely to capture, for example Cheetahs *Acinonyx jubatus* targeting less vigilant Thomson's Gazelles *Gazella thomsonii* (Fitzgibbon 1989) and Eurasian Sparrowhawks targeting small Common Redshank flocks that are close to cover (Quinn & Cresswell 2004, 2006). Any animal that behaves inappropriately in a large group or population removes any benefit of the dilution effect (Hamilton 1971), and therefore selection will always act to promote effective anti-predation behaviours, even if relatively few prey relative to the standing stock are consumed.

Alternatively, the difficulty of gathering accurate information may result in selection for minimization of risk because playing safe, if foraging conditions allow, will always be a good strategy (Sih 1992). Effective assessment of per-capita mortality rate by a prey individual relies on knowledge of rapidly changing densities and vulnerabilities of multiple predators and prey. Although likelihood of capture success should be modified by the presence of conspecifics (i.e. group size effects Elgar 1989, Cresswell 1994b) and so perception of risk should be influenced by the dilution effect (Peacor 2003), this can only operate on a very local, instantaneous level because of perceptual limitations. Therefore, perception of risk is unlikely to reflect the per-capita mortality rate at a population level over ecologically or evolutionarily relevant timescales. Indeed, the many experiments that have used predator exclosures to remove lethal effects, and then demonstrated strong non-lethal effects (e.g. Arthur *et al.* 2004), show clearly the gap between perceived predation risk (the experimental animals behave as if predators can still kill them) and actual mortality. But animals clearly can change their levels of anti-predation behaviour in response to a given level of predation risk both instantaneously (Ydenberg & Dill 1986) and over evolutionary time (Beauchamp 2004, Rodl *et al.* 2007). Therefore, future avian studies that investigate when changes in predator density and behaviour do or do not result in behavioural changes of prey are a fruitful way of determining how animals perceive predation risk, and so how non-lethal and lethal effects arise.

Responses to predation risk cannot easily be predicted

An important conclusion that arises from recognition of the importance of non-lethal effects is that non-lethal effects are more or less impossible to predict without an understanding of the natural history of the species involved or individuals' potential behavioural responses. The strength and direction of non-lethal effects has been empirically shown to depend on resource levels, stage in life history and condition of the prey (Luttbeg *et al.* 2003), as well as density of predators (Peacor & Werner 2001). Non-lethal effects have often as a consequence been identified empirically only when unexpected results arise from experiments, and there is sufficient uncontrolled variation in the experimental design to allow their exploration (Alto *et al.* 2005). For example, of 135 field experimental studies reviewed by Sih *et al.* (1985), 40% showed unexpected non-lethal effects, with vertebrates having unexpected effects more frequently than invertebrates. Although manipulative experiments on birds and mammals can potentially identify specific effects and their direction of causation, these will be so dependent on specific experimental conditions that they probably cannot be predicted in advance (Peacor & Werner 2004a). Experimental studies that attempt to do so must include, literally, pages of predictions (e.g. Schmitz 1998), and face a daunting logistical task of integrating large numbers of pairwise discrete laboratory experiments (e.g. see Relyea & Yurewicz 2002). Overall, it seems that observational studies across the range of interacting species and a range of conditions in which they interact are most likely to yield information efficiently about the relative strengths of non-lethal and lethal effects, and their consequences (Abrams 1995, DeWitt & Langerhans 2003). In practical terms this means that observational field studies (incorporating field experiments if possible) that use statistical methods to control for confounding factors are perhaps the only realistic way to study the ecological consequences of predation in birds.

Avoidance behaviour may dominate population and community ecology

There may often be little direct evidence of predators consuming prey if selection acts to favour individuals that respond to predation risk (i.e. that then show non-lethal effects) primarily by avoiding predators or by reducing their activity in a predator's presence (e.g. Sih 1986). An obvious analogy is the 'ghost of competition past': two species may apparently never compete because they occur in different areas, yet their isolation from each other now may have been a consequence of prior strong competition (Connell 1980). Indeed, some diversity in prey species may be a consequence of predators selecting for avoidance behaviour of prey, so allowing coexistence because species are forced into different realized niches. For example, foraging specificity in rodents can be determined by avoidance of Barn Owls *Tyto alba* (Brown *et al.* 1988), as well as diversity in predator species arising because of intra-guild predation (see above).

If avoidance behaviour is a common consequence of predation risk then studying the effects of predation may be difficult: the absence of direct interactions between predator and potential prey may be because avoidance prevents interaction, or simply because the potential predator does not interact at all with the suggested prey. We may only get an idea of the importance of predation when a system is perturbed by changes in ecological conditions, for example, during severe weather periods, when animals may have to prioritize foraging over predator avoidance (e.g. Cresswell 1994a, Yasué *et al.* 2003). Alternatively, but with more difficulty, we can also get an idea of the importance of the avoidance of predators by measuring reproductive costs as a result of the experimental presence or absence of predators (e.g. Peckarsky *et al.* 1993, Peckarsky & McIntosh 1998). In birds, carrying out predator removal or augmentation experiments to determine avoidance effects properly are not ethical, but 'natural' experiments such as recolonization of areas by extirpated raptors provides an opportunity to study these effects. Alternatively, habitat manipulations that affect a predator's ability to hunt, or the availability of safe foraging options, allow the fitness consequences of avoidance behaviour to be identified (Evans 2004); for example, the erecting of barriers to allow surprise attacks by Peregrines leads to avoidance of mudflat areas by Western Sandpipers (Pomeroy *et al.* 2006).

If selection acts primarily on avoidance behaviour (and this must be the default low cost, instantaneously available option for all animals faced with predation, as long as foraging is not severely compromised), then prey will never evolve completely effective anti-predation behaviours on attack because selection that acts to promote avoidance will result in reduced selection for anti-predation behaviour on attack (Brodie & Formanowicz 1991). In these circumstances there will be strong selection on predators to hunt in ways that break down avoidance. Surprise hunting is one way to do this and is a common strategy for avian predators (Cresswell 1996). Surprise hunting is usually viewed as a way for predators to get close to prey before detection, but it could be viewed as a way for predators to actually increase local densities of easy-to-catch prey (Roth & Lima 2007). In situations where avoidance is not really an option for prey, such as predators and prey inhabiting the same area more or less constantly, selection will then favour complicated behavioural and morphological prey adaptations that reduce the probability of capture during attack, and the co-evolution of predator–prey capture–escape systems such as signals of unprofitability (Caro 1986, Cresswell 1994c). Predation events therefore seem most likely to occur in situations where avoidance behaviour has broken down, for example because animals have been forced to give a high priority to reducing the risk of starvation, rather than as a result of ineffective responses to predator attacks. This means that studies of the consequences of different escape behaviours on attacks, such as how flight or crouching determines escape probability for Common Redshanks attacked by Peregrines and Eurasian Sparrowhawks (Cresswell 1993), are perhaps more interesting in terms of selection and evolution of the predator's behaviour. For the prey, selection on other behaviours, which act earlier on in the predation sequence, such as foraging efficiency allowing use of low profitability but safer sites, is perhaps much more important.

Another consequence of avoidance behaviour being widespread, with concomitant indirect effects on community ecology, is that predators should evolve ways of responding to the indirect effects they cause. For example, predators may actively reduce competitor density (i.e. intra-guild predation and avoidance – see above) because this increases their ability to hunt by surprise. Conversely, different predator species may actively associate because attempts to avoid one predator species may increase the availability of the prey for the second predator species, and vice versa (e.g. snakes and owls hunting gerbils Kotler *et al.* 1992). This means that studies that attempt to understand the distribution of predator species must consider the possibility that capacity for avoidance behaviour by their prey and their competitors may determine distribution more than actual density of prey or competitors (e.g. see Sergio *et al.* 2003).

But perhaps the most important overall point for future avian studies of predation risk with respect to predator avoidance is that strong predation selection may result eventually in little direct mortality because prey evolve to successfully avoid the predator, or evolve a phenotype that makes them unprofitable for the predator. A correlation between direct mortality and population dynamics is then only likely to be detectable in circumstances when starvation risk is so high that individuals effectively ignore predation risk (Bolnick & Preisser 2005). It might therefore be expected that lethal effects might often be low in systems where predation is *particularly* important for structuring the dynamics of populations and communities. As scientists studying predation tend to look for animals eating other animals, this may mean that much of our understanding of predation risk is biased towards systems where lethal effects dominate, and these may be far from typical.

CONCLUSION

If predation risk has important non-lethal effects on fitness, population and community dynamics, then a number of clear predictions arise that could be considered in future research into avian predation risk.

(1) Low direct mortality rates do not indicate that predators are not important to the fitness, population dynamics and community ecology of a species.

(2) Per-capita mortality rate (prey population/number eaten by the predator) will not generally indicate whether an animal will show anti-predation behaviour because predators are likely to target individuals that show less anti-predation behaviour (i.e. all individuals are not equal). Whether or not individuals respond to predators, and how much of a threat the predators represent, will be better predicted by an individual's perception of the predictability of foraging in the environment and ecological conditions that affect this and so the degree to which prey can divert resources to anti-predation behaviour and the range of anti-predation options available.

(3) High direct mortality rates are most likely to be observed under 'severe' ecological conditions, such as severe weather, environmental change, or parasite infestation when instantaneous starvation risk exceeds predation risk.

(4) When starvation risk is generally low (for example in tropical areas with low seasonality), direct mortality rates are also likely to be low, and avoidance of predation risk and its competitive effects will primarily determine density and distribution of birds.

(5) Avoidance of predation risk should be common, so that removal or introduction of predators should usually profoundly change prey, and competing non-prey distribution.

(6) Distributions of animals in the presence of predators are unlikely ever to be 'ideal' and 'free' except at a spatial scale where predation risk acts equally across patches. In most cases predators will affect the profitability of patches because those with predators will require a bird feeding there to divert some of the patch's resources to anti-predation behaviour. Consequently, where there are non-lethal effects of predation risk, habitat heterogeneity will be increased.

(7) Selection should act most strongly on foraging efficiency, or other adaptations to unpredictability of foraging opportunities, as a means of avoiding predation, rather than behaviours that reduce the probability of capture on attack. When predation risk is removed (e.g. birds on islands) then selection on foraging efficiency may be reduced, making species that have evolved in these conditions relatively poor competitors compared to species that have evolved in the presence of predators.

(8) High predation risk should correlate with prey species diversity, although this prediction is subject to the same caveat as the prediction that high competition should correlate with species diversity, namely that diversity may be a consequence of predation risk in the past.

To conclude, there are a number of ways that appreciation of the importance of the non-lethal effects should influence future studies of predation. Most importantly, predation risk should best be studied in the context of a trade-off where the diversion of resources away from long-term survival or reproduction is measured. But this approach means that we need to establish firmly how predation risk-mediated changes in intake lead to reductions in long-term survival and reproductive success. In many cases we can perhaps safely assume that diversion of resources to anti-predation behaviour reduces fitness, but there are few studies from birds to demonstrate exactly how much fitness is affected and under what ecological conditions, and so this must be a key area for future empirical research.

Measurements of lethal effects can only sometimes estimate the effects of predation, whereas measurements also of non-lethal effects, particularly via foraging rate trade-offs, will always do so. Using the foraging–predation risk (or similar) trade-off also allows us better to predict how changes in predator density will impact on population and community dynamics, and how animals perceive predation risk, because strong non-lethal effects decouple any direct relationship between predator density and direct mortality rate. Perhaps most importantly, the trade-off approach allows us to identify avoidance behaviour or changes in distribution or habitat selection as an important fitness and ecological consequence of predation risk in systems with apparently inconsequential direct predation rates.

Although the foraging–predation risk trade-off is widely studied in avian systems, its overall usefulness (because of its value in estimating non-lethal effects) for predicting population and community dynamics is probably underestimated. It therefore seems important to highlight the foraging–predation risk trade-off and its role in quantifying non-lethal effects, as well as the overall importance of non-lethal effects to the behaviour and ecology of birds: in essence, when we study predation risk in a bird species we often need to also study its foraging ecology. At the very least, consideration of non-lethal effects allows us properly to quantify predation whether we are managing populations for conservation or harvest. At the very best, non-lethal effects may provide a central unifying concept for the structuring of food webs and trophic cascades.

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