

POINT OF VIEW

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Death and danger at migratory stopovers: problems with “predation risk”

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Dierschke (2003) recently published a paper entitled, “Predation hazard during migratory stopover: are light or heavy birds under risk?” He measured the body condition of 11 species of passerine migrants depredated by feral cats and raptors at an offshore stopover site, and used these data to address two hypotheses: (1) predation risk is higher for heavy birds because it decreases the take-off ability, and (2) predation risk is higher for lean birds because their need to feed increases their exposure to predators. Dierschke found that lighter weight individuals were strongly disproportionately represented among the victims, and concluded that “it seems that the importance of reduced escape performance caused by the carrying of fuel loads is overestimated and possibly not biologically significant in terms of predation risk”. We found Dierschke’s data and analysis interesting and exciting, and believe that fundamentally, we interpret his results much as he does: lighter birds are killed disproportionately because they spend more time feeding and/or do so in “riskier” habitats. But we disagree with the inference that mass-specific “predation risk” is therefore of little ecological importance or biological significance. In this commentary we consider the reasoning behind his conclusions, focusing particularly on the meaning of “predation risk”.

Problems with “predation risk”

“Predation risk” has been used widely in the ecological literature for the past 25 years (Lima 1986), and it is becoming evident that it has various meanings. Dierschke (2003), and others, including ourselves (e.g. Burns and Ydenberg 2002), have shifted unintentionally between several possible meanings of “risk”. The use of

related terms, including, “escape performance”, “predation hazard”, “vulnerability”, “falling victim to”, “exposure to predators”, and “perceived predation risk” has further complicated matters. Exact definitions are lacking, which has allowed a variety of different meanings to march under the common term of “predation risk”.

To illustrate the definitional problem, imagine a situation in which predators hunt ground-feeding birds. The birds avoid attacks by cautious behavior, such as repeatedly scanning the environment for predators. A field ecologist studying this situation, even for a long time, might observe no or very few predation events, and could conclude that there was little “risk of predation”. But if the ground-feeding birds did not scan, the predators could catch them easily, and another field ecologist might conclude that the situation is very “risky”. This meaning refers to the probability of mortality that would occur if the birds did not scan. Thus, “predation risk” can mean quite different things. Which meaning is used has a great effect on the interpretation of what is “biologically” or “ecologically significant”.

Our primary purpose here is to outline possible meanings of terms relating to “predation risk”, and suggest a general scheme that relates them one to another. We show that the two hypotheses Dierschke considers are not contradictory alternatives, as he suggests. Rather, they address different meanings of “predation risk” that are in our view not only compatible, but complementary. We suggest that recognizing four concepts will help to clarify thinking and analysis of issues relating to “predation risk”: “mortality”, “danger”, “escape performance”, and “anti-predator behavior”. To help avoid ambiguity, we will henceforward avoid the term “predation risk” when describing what we mean.

Mortality

The most straightforward meaning and measure of “predation risk” could be the observed rate or probability of mortality due directly to predators. This usage is consistent with medical and epidemiological literature that apportions mortality among “risk factors”. This meaning is also applied in studies focusing on natural selection (e.g. Badyaev et al. 2000) and it is how Dierschke mainly uses the term in his paper.

Danger

As in the example above, a quite different meaning of predation risk is the inherent probability of becoming a prey item in any particular situation if no anti-predator measures are taken. We call this meaning of risk “danger”. Some places or times are more dangerous than others, and prey may consequently avoid them or behave more cautiously when at such sites. The level of danger is a function of inherent properties of the ecological situation, such as the abundance of predators, the existence of refuges and other aspects of the structure of the habitat, the abundance of alternative prey (including conspecifics), and other factors that the prey cannot affect directly and quickly by its behavior. One way to think about “danger” is as the mortality that would be measured in that situation if prey engaged in no (or used a standardized amount of) anti-predator behavior (cf. Brown et al. 1999). In our example with the ground-feeding birds above, “danger” is the mortality that would be measured if the birds did not scan, or were restricted to using a certain level of vigilance.

“Danger” as defined is obviously a theoretical construct and its relative value may usually have to be estimated qualitatively, though its value could be quantified in some systems. For example, Zaklan and Ydenberg (1997) showed that clams gain safety from predators such as excavating crabs and probing shorebirds by deeper burial. By extrapolating from measured mortality rates at known burial depths, danger could be estimated as the mortality of unburied clams or those buried at a defined shallow depth.

Escape performance

Many writers, including Dierschke (2003) and ourselves (e.g. Burns and Ydenberg 2002), use the word “predation risk” in a third quite different sense. Dierschke writes “That predation risk increases with increasing body mass has been shown for single birds in experiments (Witter et al. 1994, Kullberg et al.

1996, 2000)...”. In the next sentence he refers to this property of the birds as “*vulnerability*”. This meaning seems different than either mortality or danger. “*Vulnerability*” might be a reasonable term, though perhaps “*escape performance*”, which Dierschke also uses, captures more precisely what is meant: the probability of escaping capture by a predator in a standardized attack. The take-off speed experiments Dierschke cites probably come quite close to meeting this narrow definition, in that they measure the relative escape performance of individuals differing in, for example, body mass, molt intensity or wing condition. “*Escape performance*” differs from “*danger*” in that it is a property of the morphology and physiology of individual prey, whereas danger is essentially a property of the environment. Again, this is clearly a theoretical construct, but much like the notions of absolute zero in chemistry, basal metabolic rate in biology, or frictionless surfaces in physics, it is conceptually useful even if rarely met in practice.

Anti-predator behavior

Individuals use *anti-predator behavior* to adjust their probability of mortality from predators (Sih 1980, Lima and Dill 1990). The intensity of vigilance, choice of habitat or group size, or other behavior might be used for this purpose. Individuals can alter their allocation to anti-predator behavior in response to variation in their escape performance (see Fig. 2 of Ydenberg and Dill 1986) or the apparent level of danger in the environment (Ghalambor and Martin, 2002 and many other examples).

With all else equal, individuals that invest more in anti-predator activities enjoy a lower probability of mortality. Since anti-predator behavior costs something, however, organisms can be thought of adjusting their allocation to such behavior until the fitness benefits of further increase (extra safety) no longer outweigh the costs. In the case of migratory birds, these costs ultimately derive from taking longer to accumulate a given level of migratory reserves. Dierschke concludes that migrants with lower reserves took larger “risks”, (i.e. allocated less to antipredator behavior) when foraging, as we suspect also happens within our western sandpiper migratory stopover system (see below). The inference is that in both systems, delayed migration is costly. Some studies suggest that individuals vary allocation to anti-predator behavior in response to differences in apparent fitness benefits (e.g. Stillman and Goss-Custard 2002), and Dierschke’s (2003) results, in our view, reflect this variation, rather than addressing the ecological importance of escape performance (see below).

Mortality is a function of danger, escape performance, and anti-predator behavior

We consider the mortality due to predation measured in any ecological situation to result from the interaction between the intrinsic danger of the habitat (e.g. the frequency of potential attacks), the level of anti-predator behavior utilized by the prey (which affects the number of actual attacks), and the escape performance of an individual if attacked (see Fig. 1 in Lima and Dill 1990 for one mathematical formulation of this). This scheme recognizes the differing contributions to “predation risk” from the environment (e.g. habitat), an individual’s morphological state (which affects escape performance), and its behavior (anti-predator strategy).

Dierschke (2003) presented his analysis as testing alternative hypotheses, but doing so depends on conflating the “mortality” and “escape performance” meanings of “predation risk”. For the reader’s reference, we reproduce Dierschke’s statement of his hypotheses: “... predation risk is higher for heavy birds with high fuel loads, because the high wing loading decreases the take-off ability and makes *capture for predators easier*. Alternatively, lean birds are *especially prone to encounter predation* because their exposure to predators is strongly due to their urgent need for feeding ...” (italics are ours). Dierschke concluded that because heavier birds have lower mortality that “... (escape performance) ... is probably not valid in the ecological context during stopover in the wild.” He makes this assertion repeatedly: “The demonstration in this study that the lightest birds most often fell victim to predation, suggests that exposure to predators is likely to be a more important factor than escape performance.” Also, “Therefore, it seems that the importance of reduced escape performance caused by the carrying of fuel loads is overestimated and possibly not biologically significant in terms of predation risk.” These conclusions are descriptive of the results under the “measured mortality” meaning of “predation risk”. But they do not apply to its “escape performance” or “danger” meanings, which, unfortunately, Dierschke implicitly uses when setting up his first hypothesis, and many readers will assume to be his meaning in the sentences quoted above.

We agree with Dierschke that the experimental evidence he cites (Witter et al. 1994, Kullberg et al. 1996, 2000, see also Burns and Ydenberg 2002) shows that a larger fuel load reduces escape performance (slows the take off speed) of single birds. However, his expectation that poor escape performance would increase mortality did not take into account the differing behavior of light and heavy birds. An alternative interpretation of his results is that birds in better condition experienced lower mortality *in spite of* their poorer escape performance, probably *because* they invested more in anti-predator behavior. Dierschke in fact agrees with this

interpretation, if one allows for the possible alternative meanings of “predation risk”: “Whereas lean birds with urgent nutritional demands are probably more exposed, heavy birds may monitor predation risk from shelter (Koivula et al. 1995), allow for reduced foraging intensity (Fransson and Weber 1997, Moore and Aborn 2000) and thus, adjust refueling rate to the local situation of predation risk ...”.

Testing the “ecological importance” of escape performance

The structure of Dierschke’s (2003) analysis implied that the ecological importance of escape performance could be measured by the quantitative relationship between body condition and mortality rate. But this could be misleading if, as we assert, danger, escape performance, and anti-predator behavior interact. In theory, many combinations of the three could give rise to any measured level of mortality.

To assess the ecological importance of escape performance in migratory birds the key question to be addressed is not whether lighter or heavier birds are more frequently depredated, but whether individuals that base migration tactics and anti-predator behavior on their escape ability migrate more successfully than those who do not. For example, we recently reported (Ydenberg et al. 2002) that on western sandpiper migration, heavy individuals avoid a richer but more dangerous stopover site used by lighter individuals. We concluded that escape performance plays a significant role for successful migration because it so strongly affects stopover site choice. Had we been able to measure mortality with respect to condition, (which members of our group have attempted to do using novel techniques, Guglielmo and Burns 2001), we suspect that we would have found that lighter birds are disproportionately represented among the victims, because they frequent dangerous sites where falcons are able to hunt effectively using surprise, directly parallel to Dierschke’s (2003) conclusion. To evaluate the importance of escape performance itself, however, we would need to test whether a strategy of selecting stopover sites based on escape performance, which western sandpipers seem to do, or making other behavioral decisions conditional on escape performance ability, enables a more successful migration than a strategy that does not.

Ideally, such a study would involve an experimental manipulation of the behavioral decisions. This might be possible by manipulating an animal’s perception of danger levels in different environments, taking advantage of a “natural experiment” where some behavioral options were not available, such as at an isolated island where the costs of moving to alternative sites were high. A second possibility would involve using state-depen-

dent models (e.g. to explore the differential fitness of making or not making escape-performance-dependent conditional decisions in different ecological situations, Clark and Mangel 2003).

It is possible of course that, even using the above approaches, escape performance would prove not to be important on Helgoland, and that migratory systems differ in this regard. We suspect, however, that differing conclusions about the importance of “predation risk” in migratory stopover site choice lies in the uncritical use of varying meanings of “predation risk” by Dierschke and others, including ourselves.

Conclusion

The term “predation risk” has been used in the literature to refer variously and even interchangeably to any of several meanings, and this can lead to conceptual confusion. In answer to the question posed by Dierschke’s (2003) title, light and heavy birds are both “under risk”, and all else being equal, heavy birds would face a higher probability of capture. However, in this system, different levels of escape performance correlate with body condition, such that heavier birds can allocate more towards anti-predatory behavior, and thus reduce their immediate probability of mortality from predation. Distinguishing between danger from the environment, escape performance of an individual, and anti-predatory behavior as interacting determinants of mortality rate will help identify interesting questions and enable a clearer discussion of the significance of ecological processes.

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