

What determines probability of surviving predator attacks in bird migration?: the relative importance of vigilance and fuel load

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Abstract

Migrating birds must accumulate fuel during their journeys and this fuel load should incur an increased risk of predation. Migratory fuelling should increase individual mass-dependent predation risk for two reasons. First, acquisition costs are connected to the increased time a bird must spend foraging to accumulate the fuel loads and the reduced predator detection that accompanies foraging. Second, birds with large fuel loads have been shown to suffer from impaired predator evasion which makes them more vulnerable when actually attacked. Here, I investigate the relative importance of these two aspects of mass-dependent predation risk and I have used published data and a hypothetical situation for a foraging bird to investigate how much migratory fuelling in terms of escape performance and natural variation in predator detection contribute to individual risk during foraging. Results suggest that for birds foraging close to protective cover the negative impact of fuel load on flight performance is very small, whereas variation in time to predator detection is of great importance for a bird's survival. However, the importance of flight performance for predation risk increases as the distance to cover increases. Hence, variation in predator detection (and vigilance) probably influences individual survival much more than migratory fuel load and consequently, to understand risk management during migration studies that focus on vigilance and predator detection during fuelling are much needed.

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1. Introduction

Predation is clearly one of the most important evolutionary factors determining behaviour and morphology of animals (Baker and Parker, 1979; Lima and Dill, 1990). This is also of importance for migrating birds, because the acquisition of fuel load (fuelling) should increase individual predation risk due to the fact that birds must forage to accumulate the fuel and this does also result in increased time spent exposed to predators (Houston et al., 1997). Birds can also face an increased predation risk because escape performance suffers from an increased body mass resulting in

impaired predator evasion (e.g. Alerstam and Lindström, 1990; Witter and Cuthill, 1993). But the relative importance of these two aspects of mass-dependent predation risk has been very difficult to elucidate, and studies of how vigilance patterns and predator detection affect predation risk during bird migration are scarce (but see Metcalfe and Furness, 1984). Consequently, in an attempt to tease these two aspects of mass-dependent predation risk apart, I have used published data and a hypothetical situation for a foraging bird to investigate how much migratory fuelling in terms of escape performance and natural variation in predator detection contribute to individual risk during foraging (cf. Bednekoff, 1996).

Migratory passerines (Passeriformes) are generally found in various forms of cover (bushes, trees, forests) and may leave cover when foraging. When such a foraging bird is disturbed, it usually returns to cover

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swiftly and consequently it relies on cover for survival. Therefore, one important component of individual risk is the time it takes a bird to reach protective cover. This time to reach safety is a function of (1) the time it takes the bird to detect a predator and (2) the time it takes the bird to fly to cover. The second part of the function is in turn a function of the bird's fuel load, i.e. a really fat bird is slower to fly to cover than a lean bird (Kullberg et al., 1996, 2000; Burns and Ydenberg, 2002).

As described by Bednekoff (1996) a bird must not only escape from a predator attack, it must also detect the predator (see also Houston et al., 1993; Welton and Houston, 2001). Bednekoff's analysis, based on scanning behaviour of house sparrows, *Passer domesticus* (Elcavage and Caraco, 1983), emphasized the importance of the time it takes for a foraging bird to reach safety when attacked. In addition, he also suggests an accelerating relationship between the amounts of fuel a bird carries and the risk its fuel load incur. My study differs from Bednekoff's study (1996) on two important aspects: (1) I used published data on mass-dependent escape performance (Kullberg et al., 2000) to get a better estimate of how much impaired predator evasion contributes to predation risk and; (2) instead of using vigilance patterns, I used published data on how much foraging constrains predator detection (Kaby and Lind, 2003). This analysis also provides testable predictions regarding fuelling behaviour in migratory birds.

2. Methods

A bird is foraging to accumulate energy reserves and relies on cover for protection against predators. When a threat is detected the bird escapes into cover, and the time it takes for the bird to reach cover is a function of (1) how long it takes for the bird to detect the predator and (2) how long it takes for the bird to fly into cover. The time it takes for the bird to reach cover is in turn a function of its fuel load, hence this time is mass dependent.

A bird is foraging x_1 m from cover, and it takes the bird t_1 s to reach the cover. t_{detect} is how long time it takes the bird to detect an attacking predator (Fig. 1). To estimate the effect of detection on predation risk, I used observed variation in predator detection in blue tits foraging for live insect prey (Kaby and Lind, 2003). This distribution did not differ from normality (Lilliefors test for normality, $p = 0.2$). Mean detection time was 0.91 ± 0.38 SD ($n = 45$). Hence, birds within 1 standard deviation (i.e. 68% of the birds) from the mean detected the predator between 0.53 (1 SD below the mean) and 1.29 s (1 SD above the mean) and birds within 2 SDs (i.e. 95% of all the birds) detected the predator approximately between 0.15 and 1.67 s. Values of predator detection (1, 2 and 3, SD, respectively) were used to

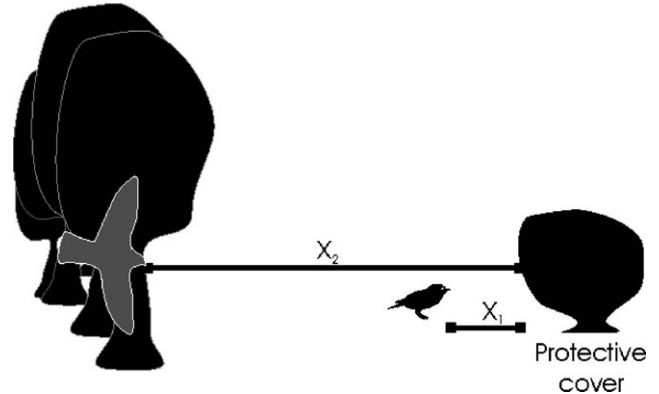


Fig. 1. The hypothetical predator–prey interaction used in this study. t_1 is the time it takes the prey bird to reach cover which is a function of the time it takes to detect the attacking predator and the time it takes the prey bird to fly to the protective cover. t_2 is the time it takes the predator to reach the protective cover.

relate the effect of detection to the effect of fuel load on predation risk.

Let t_{escape} be the time it takes for the bird to fly into cover and this is a function of the bird's mass-dependent escape speed, where h depicts fuel load of a bird. I used the linear relationship from a take-off study of migrating sedge warblers *Acrocephalus schoenobaenus* (Kullberg et al., 2000). Using this study $t_{escape} = x_1 / (-0.01 \times h + 2.59)$. This relationship comes from sedge warblers' escape speed after a distance of 60 cm has been covered. Then, $t_1 = t_{detect} + t_{escape}$. To estimate how risk is influenced by fuel load I used different fuel loads, from lean birds carrying no extra weight to extremely fat birds carrying 80% fuel of lean body mass. Both the variation in predator detection and the variation in fuel load used in this simple model are biologically relevant and are not exaggerations.

To relate this hypothetical bird's performance to a predator attack, let t_2 depict the time it would take a hypothetical hawk *Accipiter* sp. to reach the protective cover from an attack launched at the speed v from a nearby forest edge (Fig. 1). It was then assumed that if the hawk reaches cover before the prey bird, the prey bird is killed. In this example the distance from the forest edge to the foraging bird was set to 5 m, and x_1 was set to 1.5 m which makes the distance x_2 6.5 m in total. The hawk's time to protective cover is then, $t_2 = x_2 / v$. Hawks from the genus *Accipiter* are important predators on nearly all small passerine birds and have been observed attacking prey at 5–28 m/s (Goslow, 1971; Hilton et al., 1999).

3. Results and discussion

This simple model of a predator–prey interaction highlights some important conclusions regarding

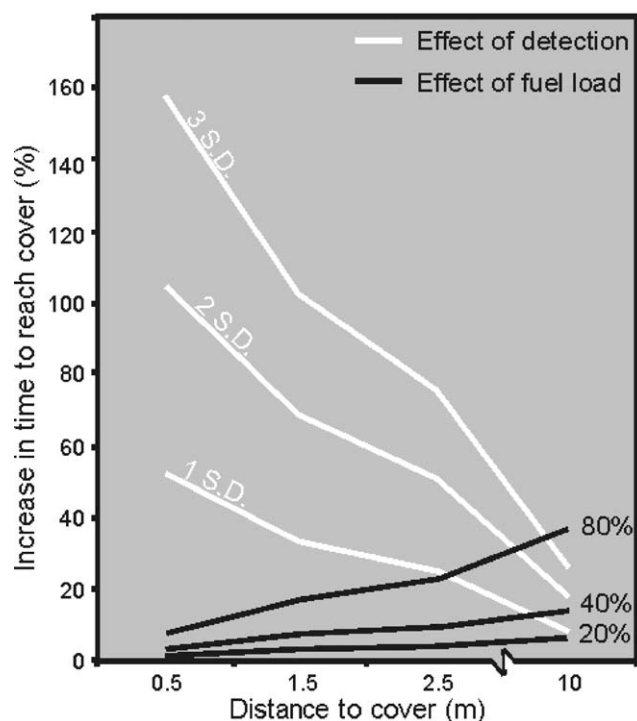


Fig. 2. The impact of predator detection and fuel load on the time it takes a bird to reach protective cover. The effect of variation in detection is depicted by white lines. The different lines illustrate how much later a bird reaches cover if detection is prolonged by one, two or three SD from a bird detecting the predator 1 SD earlier than the mean. The effect of fuel load is depicted by black lines. The different lines illustrate how much later a bird reaches cover when the fuel load is 20%, 40% or 80% of lean body mass. Note that the x-axis is broken.

predation risk during foraging. First, it suggests that the variation in predator detection is more important than fuel load for a foraging bird in determining the probability of survival when it is attacked (Fig. 2), especially when a bird is foraging close to cover. A conservative example supports this conclusion. A bird detecting the predator 1 SD later than the mean (1.1 s to reach cover with mean detection time being 0.9 s) it needs 1.48 s to reach cover 0.5 m away (i.e. 34% longer time to cover). Whereas if this bird is carrying a huge fuel load of 80% fuel of lean body mass it will need 1.2 s to reach the same protective cover (i.e. 8% longer time to cover than 1.1 s, the time it takes a lean bird to reach cover at mean detection). Hence, variation in predator detection should influence individual survival of predator attacks more than migratory fuel load and consequently, to understand individual risk management during migratory fuelling studies that focus on vigilance and predator detection during fuelling are much needed. In addition, this also suggests that the most important aspect of mass-dependent predation risk during fuelling is how long time a bird spends exposed to predators, rather than how much slower a fat bird flies away. Important to note is that the conclusions

from this study are rather different from that of Bednekoff (1996). This is mostly explained by the estimates of bird flight performance that were used, and the relationship between fuel and escape flight from the study on sedge warblers gives a more accurate estimate than the study on routine flights by zebra finches (Metcalf and Ure, 1995; see Veasey et al., 1998 for a detailed discussion on routine vs. escape flights). However, this study corroborates his suggestion that small changes in time to reach cover is likely to have a large effect on predation risk, even though these differences may largely be due to variation in predator detection instead of how large fuel load a bird carries.

It is important to note that the information I needed for this theoretical treatment could not be found for one and the same species. Hence, I chose the sedge warbler study to estimate mass-dependent escape speed because this study has reported the strongest negative relationship between fuel and flight, which makes my conclusions in this paper conservative. Then I chose the blue tit data for predator detection for two reasons: (1) the situation of a bird foraging on insect prey is biologically relevant for many species of migratory passerines, and (2) I had access to the data enabling me to use the important estimates of variation in predator detection. That the variation in time to detection used in this investigation is biologically relevant becomes evident when examining different taxa in the literature. Instead of detection time, one can examine interscan intervals as in Bednekoff (1996), that is the time between two consecutive scans when an animal is supposed to be poor at detecting a predator (but see Lima and Bednekoff, 1999; Kaby and Lind, 2003). Lendrem (1983) reports that more than 50% of all interscan intervals in blue tits are longer than 2 s. Downy woodpeckers *Picoides pubescens* foraging on their own take 1–5 s between scans (Sullivan, 1985) and it can be worth mentioning that northern bobwhites *Colinus virginianus*, even when in groups of four, took approximately 2 s to respond to an incoming predator model (Williams et al., 2003).

The effect of increased time exposed to predators has not yet been addressed by empirical bird migration research, although it has been suggested that fat birds are more eager to leave a risky patch when exposed to an increased predation risk than are lean birds (Fransson and Weber, 1997). The negative effect of migratory fuel load on escape performance has been shown for both passerines (Passeriformes, Kullberg et al., 1996; Lind et al., 1999; Kullberg et al., 2000) and waders (Charadriiformes, Burns and Ydenberg, 2002). Even though these studies show that fat birds escape slower or in shallower angles, no quantitative conclusions regarding the relative importance of migratory fuel load on predation risk has emerged from these studies. Instead, Dierschke (2003) found that birds falling victim

to predators at a small island in the North Sea were mainly birds with small fuel loads indicating that birds in poor condition forced to forage suffer from exposure to predators whereas heavy birds could stay put and hide in safety to await the night when they continue their migratory journey. Importantly, many of the investigated species do not probably accumulate any significant amount of fuel at this site, hence these data cannot be used to draw general conclusions regarding mass-dependent predation risk during migratory refuelling (see Lank and Ydenberg, 2003 for a more detailed discussion).

When introducing a hypothetical predator it becomes even more evident that the risk a bird foraging close to cover faces is strongly related to when the predator is detected. At a normal attack speed (above 10 m s^{-1}) birds detecting the predator 1 or more SD later than the mean will always be killed, regardless of the predator's distance to the prey (2–10 m), whereas the impact of fuel load does not contribute to such a qualitative effect (Fig. 3). Because the time it takes for the predator to reach the prey increases steeply when attack speed is reduced this suggests that the negative effect of fuel load

is reduced even more when attack speed is reduced. In addition to escape speed, a bird's manoeuvrability is also important when escaping from predators and this should also be affected by increasing fuel load (Hedenström, 1992). For example, to dodge in the last moment is an important anti-predator strategy for birds (Lima, 1993; Lind et al., 2002), but even though manoeuvrability was excluded from this investigation, judging from Fig. 3 it appears likely that many birds killed by raptors never detect the incoming threat.

Even though the model did not examine mortality per distance en route (see Alerstam and Lindström, 1990 for how to minimize mortality per distance covered) but instead probability of surviving attacks during foraging, this study suggests that predation risk results from an interaction between fuel load and distance to cover (cf. Bednekoff, 1996). This interaction, which also lacks empirical treatment, has both intra- and interspecific implications. Individuals within a species can thus be expected to show flexibility in microhabitat choice during fuelling, and fat birds should be more reluctant to forage far away from cover than lean birds, since the effect of fuel load increases with increasing distance to cover. Because the impact of fuel load on predation risk will increase with increasing distance to cover another testable prediction emerges which suggests that species living out in the open (e.g. wagtails and pipits, Motacillidae), which are more dependent on their flight to evade predators, should migrate with smaller fuel loads than birds spending their time inside or close to protective cover. Of course, this last prediction should not hold where and when birds are forced to fuel up extensively, for example prior to crossing a barrier (Fransson et al., 2001; Rubolini et al., 2002). We can therefore expect that the evolution of fuelling behaviour should be affected by this interaction.

It is well known that birds regulate their body mass according to the prevailing predation risk, and this study suggests that, at least for species which relies on protective cover, it is not due to the effect on escape performance, but more likely serving the end of minimizing acquisition costs of fuel, for example the time spent exposed to predators.

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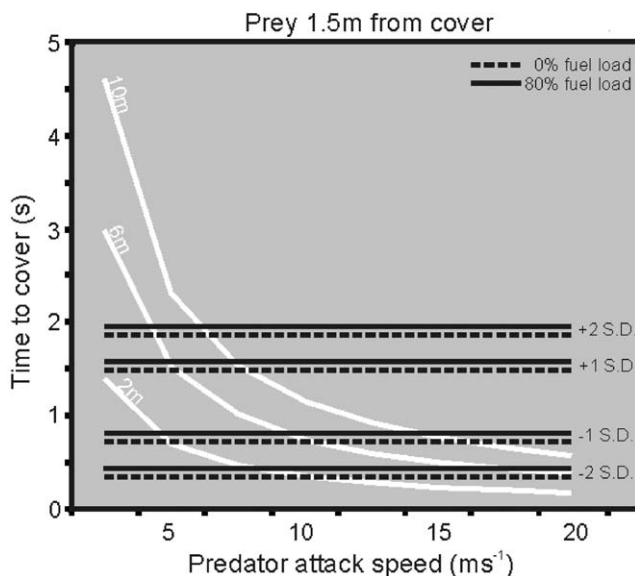


Fig. 3. This graph depicts hypothetical predation risk for a bird when attacked by a predator launching its attack from different distances to cover and at different speeds. It is assumed that if the predator reaches cover before the prey the attack will be successful. Hence, at any y -value, if the x -value of the predator's line (white lines) is below a horizontal prey line (black lines) the prey with those particular characteristics (with respect to predator detection and fuel load) is dead because the predator reached the cover before the prey. The distance from the predator to the prey bird is given above each white line. Dashed lines show the time it takes to reach cover for lean birds, and solid lines show how long time it takes a bird carrying a fuel load of 80% of lean body mass to reach cover. Note that the lines depicting prey time to reach cover is simply the calculated estimates for a prey bird foraging 1.5m from protective cover.

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