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Anti-predation behaviour during bird migration; the benefit of studying multiple behavioural dimensions

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Abstract Predation and predation risk have recently been shown to have profound effects on bird migration, but we still know relatively little about how birds respond to predation risk en route and how this is translated into fundamental aspects of optimal migration. Here, we make the case that to understand the fitness consequences of foraging and anti-predation behaviour en route we cannot rely on single behaviour relationships but must take many aspects of behaviour into account, because of predation risk compensation. We show this in a case study of fat and vigilant birds feeding close to cover, which emphasises the importance and potential of predation risk compensation. Another reason for taking many aspects of behaviour into account is that different behaviours need not contribute equally to individual fitness. Birds faced with an increased predation risk during migration can compensate for increased predation risk in different ways. This implies that the adaptive value of a behavioural trait can still be ambiguous even if a survival cost can be correlated with particular behaviour where all other things are equal (e.g. in an experiment). That is because in natural systems there may frequently be many other ways for animals to compensate, because all other things are never equal, so that the particular behaviour can actually be of little consequence to individual fitness. In conclusion, when studying foraging decisions and anti-predation behaviour during stopover potential compensatory mechanisms should be incorporated. This knowledge is also critical for improving future models of optimal migration.

Keywords Anti-predation behaviour · Predation · Fuelling · Vigilance · Behavioural compensation

Introduction

To an individual, apart from reproducing successfully, the most important issue is to survive. The dangers en route have recently been estimated and it has been suggested that mortality rates for the New World migratory songbird the black-throated blue warbler, *Dendroica caerulescens*, are up to 15 times higher during migration than during the stationary periods of summer and winter. In addition, more than 85% of their measured apparent mortality occurred during the migratory period (Sillet and Holmes 2002). Lindström (1989) has also estimated that during six weeks of autumn migration in Southern Sweden, 10% of all chaffinches (*Fringilla coelebs*) and bramblings (*F. montifringilla*) at one stopover site were killed by birds of prey (mostly by sparrowhawks *Accipiter nisus*). Other recent studies on sandpiper migration also suggest that the dangers of migration can have a profound impact on the evolution of migration strategies (Lank et al. 2003; Ydenberg et al. 2004). The scheduling of moult and migration during autumn in three North American shorebirds might have evolved to avoid encounters with migratory peregrine falcons *Falco peregrinus*. These studies imply that anti-predation behaviour en route are important to individual fitness and that we need to understand more about how migratory birds cope with the risk of predation to understand the hows and whys of bird migration in general (see also Lindström 1989).

Here we aim to emphasize that to understand the role of predation risk during bird migration we must incorporate multiple dimensions of anti-predation behaviour, especially when studying stopover behaviour. We believe we have reached as far as we can by simply studying a single aspect of behaviour when all other things are equal. This is because while an individual bird is behaving in a way that seems, to the observer, to incur

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high predation risk the same bird may in fact compensate fully for that observed risky behaviour in another dimension of behaviour. We discuss how the study of stopover ecology can benefit from incorporating multiple dimensions of behaviour and we illustrate this using a case study of mass-dependent predation risk (Lind 2004) or, as it can be referred to in bird migration, the cost of being fat. Finally, because the outcome of anti-predation behaviour can be translated into foraging decisions made by individual birds, understanding how individual birds cope with the dangers en route will help us understand how birds manage their stopovers in terms of fuel deposition rate, departure load, and stopover duration—three central issues in the study of optimal migration (e.g. Alerstam and Lindström 1990, Hedenström and Alerstam 1997).

Multiple dimensions of predation risk during foraging: what's the problem?

We believe there are two major problems with studying one aspect of behaviour in isolation in terms of understanding anti-predation behaviour during stopover in bird migration.

First, as mentioned above, behaviour that in isolation might appear to incur a high predation risk to an individual bird might in reality be compensated for fully by alternative behaviour. The logic of predation risk compensation is shown in Fig. 1. According to theory, predation risk should increase with increasing fuel load, for example because of impaired predator evasion (as suggested by Blem 1975). If, however, there are resources to allocate to alternative behaviour (e.g. vigilance which aids predator detection) the increased risk incurred as a result of impaired predator evasion might, in fact, be compensated for and there will consequently be no net increase in predation risk caused by mass-dependent predator evasion. There are no empirical studies that have shown this in birds, but a similar situation has been investigated in a lizard, the Southern water skink (*Eulamprus tympanum*). Female lizards increase substantially in mass during reproduction, because of egg

load, and, as with fuel load in migratory birds, this extra weight has been shown to impair their ability to escape (Cooper et al. 1990; Schwarzkopf and Shine 1992). Hence, one might conclude that gravid female lizards should be more vulnerable to predation than non-gravid females because they are less adept at escaping from predators. But, because of predation risk compensation, gravid females have been shown to be no more susceptible to predation than non-gravid females, mainly because they behave more cryptically thereby escaping detection by visually hunting predators (Schwarzkopf and Shine 1992; see also Pérez-Tris et al. 2004).

Second, it is imperative that one takes more than one aspect of behaviour into account when studying anti-predation behaviour during stopover, because different aspects of behaviour are unlikely to contribute equally to individual fitness. If a bird can compensate for high fuel load by increasing vigilance, it is obvious that to understand anti-predation behaviour en route one has to take vigilance into account. If vigilance (or any other behaviour) is a more important determinant of surviving predator attacks at stopover than fuel load, then individual vigilance is likely to contribute more to individual fitness than if the bird alters its body mass in response to predation risk (Fig. 2). To illustrate the importance of incorporating multiple dimensions of behaviour to enable understanding of how different factors determine individual fitness we turn to ducks (Anatidae). In many studies in avian ecology fledging success is used as a proxy for fitness. A study for three duck species (Anatidae) of 22 years of data on different factors usually believed to be important for individual fitness showed, however, that fledging success does not have to be related to fitness (Blums and Clark 2004). They measured life-time reproductive success (LRS) and revealed that fledging success was strongly related to LRS in one species only. Instead, the best predictor of LRS was how many times a female tried to breed (i.e. longevity).

Multiple dimensions of predation risk during foraging: a case study

Because migrating birds need fuel to travel we must identify the costs of energy acquisition and the associated costs of carrying the fuel loads. First, to build up fuel loads birds must forage, and during foraging birds are exposed to predators (e.g. Houston et al. 1997). Predation risk during foraging varies with several factors, e.g. foraging task (Kaby and Lind 2003), group size (Kenward 1978; Cresswell 1994b), and habitat choice (Lindström 1990; Hinsley et al. 1995). Second, the cost of carrying fuel loads can also incur increased predation risk, either:

- 1 because the fuel load is energetically costly to carry, resulting in fat birds being forced to spend more time

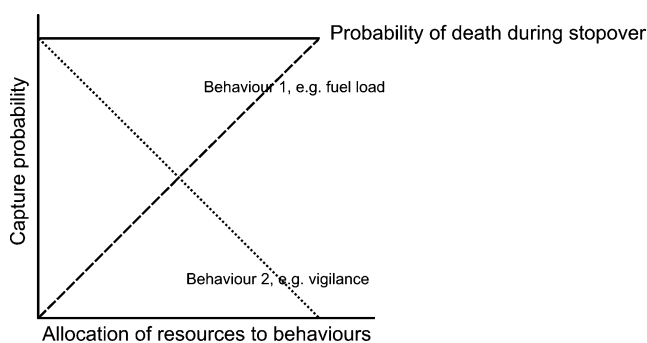


Fig. 1 An example of predation risk compensation. Behaviour believed to result in increased risk of predation (carrying a high fuel load) might, in fact, be fully compensated by another aspect of behaviour (e.g. increased vigilance)

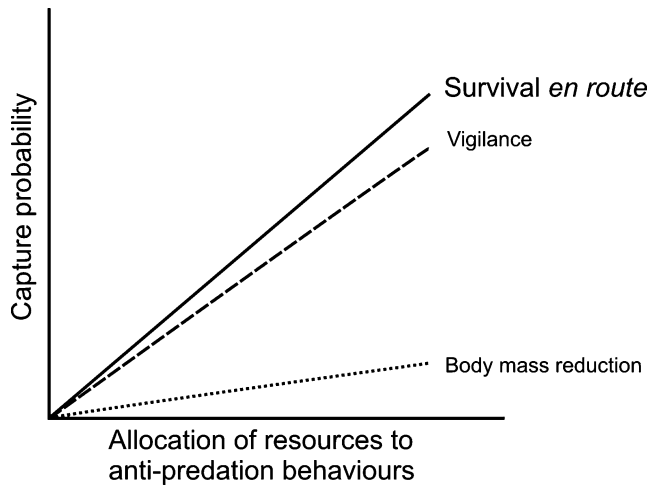


Fig. 2 It is also important to study multiple aspects of behaviour, because these are unlikely to contribute equally to individual fitness

foraging thereby compensating for the physiological cost of being fat (e.g. Lindström and Rosén 2002); or 2 because birds with large fuel loads are less adept at escaping attacking predators (e.g. Blem 1975).

The important point is that even though we can establish that fat birds fly more slowly (Kullberg et al. 1996; Burns and Ydenberg 2002) and/or at lower escape angle (Lind et al. 1999) this information is not enough to draw conclusions about how predation risk varies with fuel load or how fuel load determines predation risk or predation per second (section above and Figs. 1, 2). This is because foraging behaviour per second can vary with fuel load and instead of paying a cost of predation, a heavy migrant may instead forage more safely and trade the predation cost against a time cost by, for example, increasing vigilance. As a result, a small modification of vigilance behaviour could then compensate fully for the previously assumed elevated predation risk because of an increased fuel load. This is best illustrated with an example (from Lind 2004).

In a theoretical investigation Lind (2004) used published data and a hypothetical situation for a foraging bird to explore how much impaired escape performance and variation in predator detection contribute to individual risk during foraging. The relative importance of migratory fuel load was, surprisingly, very small when birds forage near cover because a small change in vigilance can override the negative effect fuel load has on the time it takes the bird to escape into cover. In essence, the natural variation in escape flight ability is minute in comparison with natural variation in predator detection. A massive fuel load (80% fuel of lean body mass) only increased the time it took the bird to reach protective cover half a meter away, when attacked, by a mere 8%, whereas if the same bird detects the predator one standard deviation later than the mean it needed 53% longer to reach the protective cover (Fig. 3). This implies that vigilance, and consequently variation in predator

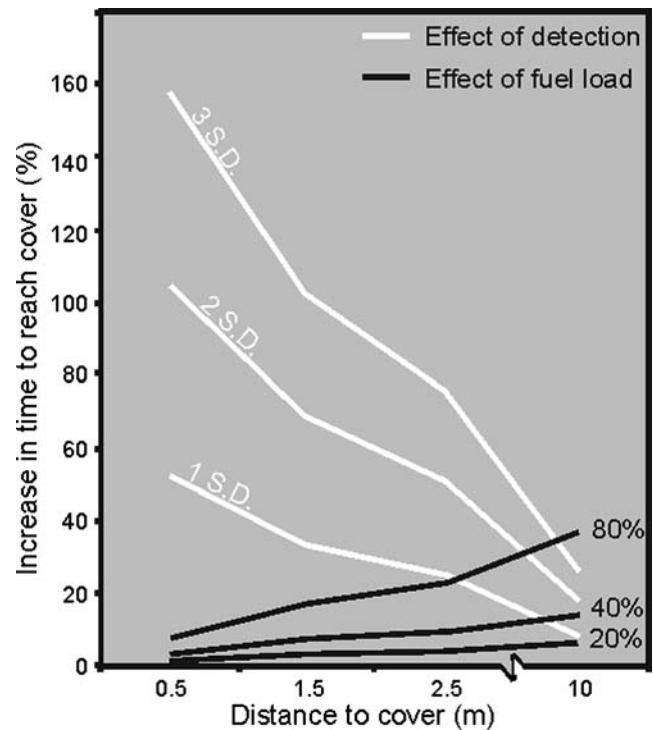


Fig. 3 The relative importance of fuel load and predator detection is shown here. *Black lines* indicate how much fuel load will affect the time it takes a prey bird to reach cover when it carries an amount of fuel different from that carried by a lean bird (fuel loads of 20, 40, and 80% fuel of lean body mass). *White lines* indicate how much the time to reach cover depends on predator detection when the bird detects a predator 1, 2, and 3 SD later around the mean. Reprinted from Lind, © 2004, with permission from Elsevier

detection, probably affects individual survival during foraging much more than migratory fuel load.

When a hypothetical predator was put into the model the same result was found, that the time it takes a bird to reach protective cover is nearly exclusively because of variation in predator detection, and consequently in vigilance, rather than mass-dependent flight performance. As an illustrative example, take a predator attacking at 10 m s^{-1} or faster, it would always kill a bird that was slow to detect the predator (a bird that detects the predator 1 SD later than the mean), irrespective of the distance of the predator from the prey bird and the fuel load of the prey bird (Fig. 4).

Importantly, the results from this study are quite conservative even though they show such a small effect of fuel load on the probability of surviving predator attacks. The model is based on the steepest negative relationship found between escape flight ability and fuel load (Kullberg et al. 2000) whereas the data on predator detection in the model come from a study in which the prey birds were relatively quick at detecting the predator (Kaby and Lind 2003) as compared with other studies on vigilance in birds. Therefore, if tested in the field, it is likely that the effect of vigilance would be even greater and the effect of fuel load even smaller.

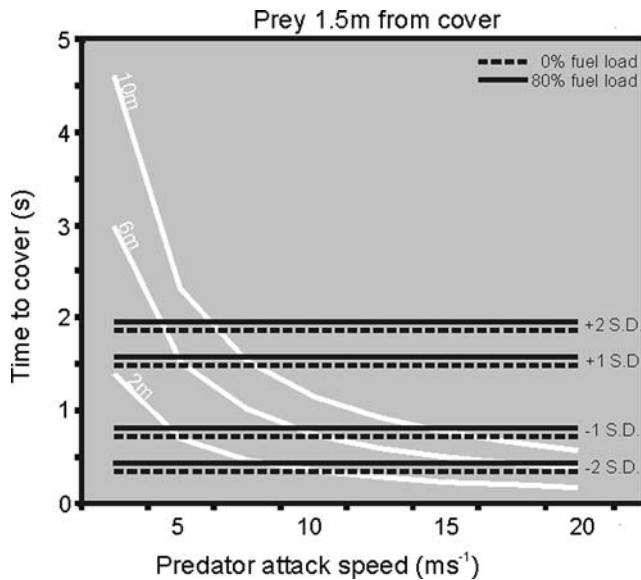


Fig. 4 This graph depicts the relative importance between fuel load and predator detection when a hypothetical predator has been put into the model. The predator launches an attack from different distances (2, 6, and 10 m) at different speeds (2.5–20 m s⁻¹). If one assumes the prey bird will be taken by the predator if the predator reach the cover before the prey, then for given x and y values the prey will be killed if the predator's *white line* is below the prey's *black lines*. The time it takes a lean bird to reach protective cover is indicated by *dashed black lines*, and this time for birds carrying a massive 80% fuel load of lean body mass is indicated by *solid black lines*. This given scenario is for a bird that forages 1.5 m from protective cover. Reprinted from Lind, © 2004, with permission from Elsevier

Most migratory songbirds prefer habitats with vegetation and lead their lives close to cover, which they may leave during foraging bouts. When disturbed they usually use the cover as their escape destination thereby seeking protection from attacking predators. It might seem reasonable that a bird with impaired escape ability will be more likely to fall victim to an attacking predator because the probability of surviving an attack depends on the time it takes the prey bird to reach the cover. But the important point is that we must take more than one dimension of behaviour into account, because predation risk varies with more than just this one factor. Hence, a laboratory-based quantification of escape ability can be of little consequence for individual fitness under natural conditions. The main reason for this is that the probability of surviving a predator attack may depend more on whether or not a bird at stopover detects the predator, rather than how swiftly it can evade the attack. It should be noted that predation risk compensation for high fuel loads does not necessary have to be related to vigilance. A fat bird can potentially compensate in many other ways, by for example choosing a safer foraging site (Hinsley et al. 1995), foraging on prey that is easy to handle (Kaby and Lind 2003), or, perhaps, compensate for the increased wing loading physiologically, by increasing the strength of their flight muscles (Lindström et al. 2000; Lind and Jakobsson 2001).

Another implication of this study is that as the prey bird forages further away from cover the importance of escape performance increases, at least if the bird is carrying very large fuel loads (approximately above 40% fuel load of lean body mass). This could have important implications for birds living in very open habitats, for example shorebirds. So, according to this model, impaired predator evasion because of extensive fuelling should be far more important for shorebirds than for most passerine migrants leading rather secluded lives in or near protective cover. Shorebirds may, however, still compensate behaviourally for an increased fuel load in other ways, for example by avoiding predators spatially (Ydenberg et al. 2002) or temporally (Lank et al. 2003) or by joining larger groups (Cresswell 1994b).

Importantly, this study does not, however, reject the hypothesis that migrating birds will suffer from mass-dependent predation risk (Lank and Ydenberg 2003) because mass-dependent predation risk can be mediated in different ways. Although this study suggests that birds are unlikely to suffer from increased mortality during migration, because of mass-dependent impaired predator evasion, increased fuel load will increase metabolic cost and hence force fat birds to forage more extensively thereby exposing them to hunting predators. This also puts refuelling birds at risk, because a bird must forage to be able to accumulate the much needed fuel loads. We do, however, believe that mass-dependent predation risk mediated by impaired escape performance is unlikely to be an important determinant of mortality during fuelling, which has been suggested in earlier studies of escape flight performance (Kullberg et al. 1996; Lind et al. 1999; Kullberg et al. 2000), especially not in migratory passerines living in or near cover (Lind 2004).

Discussion

Few studies have taken more than one aspect of behaviour into account when trying to understand how predation risk en route affects stopover decisions. The ultimate goal for a bird on stopover is to replenish its fuel stores, enabling it to leave the stopover site and continue migration. A bird cannot replenish its fuel stores without foraging, and for migratory birds the level of risk taking is elevated (Moore 1994). Because it is well known that animals alter their foraging to take the prevailing predation risk into account (reviewed in Lima 1998b) and that increased activity increases mortality in general (Sih 1986; Anholt and Werner 1995; Wisenden et al. 1999; Downes 2002; Biro et al. 2003) we need to understand more about how predation risk alters foraging decisions in migratory birds. This is especially important because individual foraging decisions underlie the three central aspects of optimum migration, that is fuel deposition rate, stopover duration, and departure fuel load (Alerstam and Lindström 1990). We know very little about how predation risk affects these decisions. We know that fuel deposition rate, but not stopover

duration, of wheatears *Oenanthe oenanthe* is affected by predation risk (Schmaljohann and Dierschke 2005). In an experiment, blackcaps *Sylvia atricapilla* altered their fuel deposition rate when predation risk was increased by exposing them to a stuffed sparrowhawk, *A. nisus* (Fransson and Weber 1997). In addition, including changes in the migratory restlessness of birds in predation risk treatment also suggests that blackcaps might alter their stopover duration because of elevated predation risk. It has been suggested that western sandpipers *Calidris mauri* have reduced their stopover duration and carry less fuel at stopover sites in British Columbia because of the greater predation risk from the larger number of peregrine falcons in the area during autumn migration (Ydenberg et al. 2004). These few studies are, however, obviously insufficient for us to draw general conclusions about how anti-predation behaviour during stopover affects foraging decisions.

In their influential optimality model Alerstam and Lindström (1990) formulated three fundamental hypotheses derived from their model of optimum migration. These hypotheses suggest that migrants are selected for minimising time, energy, or mortality during migration. In the “mortality” model birds are assumed to minimise mortality per distance covered, and this rate of mortality is assumed to be largely dependent on departure fuel loads, with higher fuel loads incurring higher mortality. Mass-dependent predation risk has been a well-studied phenomenon outside the topic of bird migration for the last 20 years and it was set in motion with the first theoretical treatment by Lima (1986) when he postulated the optimum body mass theory. We now know that birds regulate their body mass in respect of predation risk; the most common pattern is that birds reduce their body mass as a response to increased risk of predation (Gosler et al. 1995; Lilliendahl 1997; Carrascal and Polo 1999; van der Veen 1999; Piersma et al. 2003). But the fact that similar studies have shown that birds might increase their body mass in response to increased predation risk (Fransson and Weber 1997; Lilliendahl 1998; Pravosudov and Grubb 1998) shows that behaviour other than regulation of body mass must be incorporated for us to understand what the birds optimise during foraging and refuelling. Although it is assumed in the optimum migration models that the level of fuel load is the most important determinant of mortality during bird migration, we do not know whether this is true. We do know, however, that activity (e.g. Sih 1986; Anholt and Werner 1995; Wisenden et al. 1999; Downes 2002; Biro et al. 2003), which might be analogous to fuelling rate, vigilance (Fitzgibbon 1989), and habitat choice (Cresswell 1994a; Hinsley et al. 1995; Whitfield 2003) all are important factors affecting individual survival in animals. In addition, animals can compensate for the increased predation risk incurred as a result of higher body mass by behaving cryptically (Schwarzkopf and Shine 1992) or simply by modifying vigilance (Lind 2004). Such non-lethal effects predators have on prey do not only affect

individuals but can also have profound population consequences for prey animals (reviewed in Lima 1998a; see also Peacor and Werner 2001; Ydenberg et al. 2004). We therefore believe that future studies of fuelling behaviour during stopover must first recognise that migratory birds may compensate behaviourally, thereby confounding any single behaviour relationship, and then identify what factors determine mortality during migration. Such studies are important for our understanding of what governs fuel deposition rate, stopover duration and departure loads, but they are also of great importance for improving future models of optimal migration.

We conclude that the adaptive value of a behavioural trait can still be ambiguous even if survival cost can be correlated with a particular behaviour where all other things are equal (e.g. in an experiment). This is because in natural systems there may frequently be many other ways for animals to compensate, because all other things are never equal, so particular behaviour can actually be of little consequence for individual fitness. This was shown by the case study outlined above of fat and vigilant birds feeding close to cover, which emphasises the importance and potential of predation risk compensation and that we need to acknowledge that different behaviour does not necessarily contribute equally to individual fitness (Lind 2004). Birds faced with an increased predation risk during migration can compensate for this in different ways. They can, for example, join a larger flock (Lindström 1989), change patch (Lindström 1990; Ydenberg et al. 2002), and/or allocate more time to anti-predation behaviour (Schmaljohann and Dierschke 2005). In conclusion, when studying foraging decisions and anti-predation behaviour during stopover these potential compensatory mechanisms should be incorporated.

Zusammenfassung

Zum Vorteil der komplexen Verhaltensanalyse bei Untersuchungen zum Räuberabwehrverhalten von Vögeln während des Zuges

Predation und Predationsrisiko haben wichtige Auswirkungen auf den Vogelzug, doch wissen wir bisher immer noch recht wenig darüber, wie Vögel während des Zuges auf ein Predationsrisiko reagieren und welche Konsequenzen dies für den optimalen Zugablauf hat. Wir können zeigen, dass es für ein besseres Verständnis der Fitnesskonsequenzen von Ernährungsverhalten und Feindabwehrverhalten nicht ausreichend ist, nur einfache Verhaltensbeziehungen zu betrachten, sondern dass es eines vielfältigeren Ansatzes bedarf, da Predationsrisikos kompensiert werden kann. Ein anderer Grund für komplexere Verhaltensanalysen ist, dass einzelne Verhaltensweisen nicht gleichmäßig zur individuellen Fitness beitragen. Vögel, die während des Zuges einem

erhöhten Predationsrisiko ausgesetzt sind, kompensieren dieses in unterschiedlicher Weise. Dies bedeutet, dass der Anpassungswert eines bestimmten Verhaltens vieldeutig sein kann, auch wenn es eng mit der Überlebensrate korreliert und alle anderen Faktoren im Experiment konstant gehalten sind. Dies hat seine Ursache darin, dass im natürlichen Umfeld viele andere Möglichkeiten bestehen, Predationsrisiko zu kompensieren, da dort niemals alle anderen Faktoren unverändert sind. Dadurch kann ein bestimmtes, aktuelles Verhalten nur von geringer Bedeutung für die individuelle Fitness sein. Dies heißt, dass bei Untersuchungen zur Ernährung und zum Feindabwehrverhalten von Vögeln in zeitlichen Rastgebieten solche komplexen kompensatorischen Mechanismen berücksichtigt werden müssen. Dies hat auch wichtige Einflüsse für die zukünftige Formulierung von Modellen zur optimalen Zugweise.

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References

- Anholt BR, Werner EE (1995) Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* 76:2230–2234
- Biro PA, Post JR, Parkinson EA (2003) From individuals to populations: prey fish risk-taking mediates mortality in whole system experiments. *Ecology* 84:2419–2431
- Blem CR (1975) Geographic variation in wing-loading of the house sparrow. *Wilson Bull* 87:543–549
- Blums P, Clark RG (2004) Correlates of lifetime reproductive success in three species of European ducks. *Oecologia* 140:61–67
- Burns JG, Ydenberg RC (2002) The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). *Behav Ecol Sociobiol* 52:128–136
- Carrascal LM, Polo V (1999) Coal tits, *Parus ater*, lose weight in response to chases by predators. *Anim Behav* 58:281–285
- Cooper WE Jr, Vitt LJ, Hedges R, Huey RB (1990) Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. *Behav Ecol Sociobiol* 27:153–157
- Cresswell W (1994a) Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *J Anim Ecol* 63:589–600
- Cresswell W (1994b) Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Anim Behav* 47:433–442
- Downes SJ (2002) Size-dependent predation by snakes: selective foraging or differential prey vulnerability? *Behav Ecol* 13:551–560
- Fitzgibbon CD (1989) A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Anim Behav* 37:508–510
- Fransson T, Weber TP (1997) Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. *Behav Ecol Sociobiol* 41:75–80
- Gosler AG, Greenwood JJD, Perrins C (1995) Predation risk and the cost of being fat. *Nature* 377:621–623
- Hinsley SA, Bellamy PE, Moss D (1995) Sparrowhawk *Accipiter nisus* predation and feeding site selection by tits. *Ibis* 137:418–420
- Houston AI, Welton NJ, McNamara JM (1997) Acquisition and maintenance costs in the long-term regulation of avian fat reserves. *Oikos* 78:331–340
- Kaby U, Lind J (2003) What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? *Behav Ecol Sociobiol* 54:534–538
- Kenward RE (1978) Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *J Anim Ecol* 47:449–460
- Kullberg C, Fransson T, Jakobsson S (1996) Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proc R Soc Lond B* 263:1671–1675
- Kullberg C, Jakobsson S, Fransson T (2000) High migratory fuel loads impair predator evasion in sedge warblers. *Auk* 117:1034–1038
- Lank DB, Butler RW, Ireland J, Ydenberg RC (2003) Effects of predation danger on migration strategies of sandpipers. *Oikos* 103:303–319
- Lank DB, Ydenberg RC (2003) Death and danger at migratory stopovers: problems with “predation risk”. *J Avian Biol* 34:225–228
- Lilliendahl K (1997) The effect of predator presence on body mass in captive greenfinches. *Anim Behav* 53:75–81
- Lilliendahl K (1998) Yellowhammers get fatter in the presence of a predator. *Anim Behav* 55:1335–1340
- Lima SL (1986) Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377–385
- Lima SL (1998a) Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48:25–34
- Lima SL (1998b) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv Study Behav* 27:215–290
- Lind J (2004) What determines probability of surviving predator attacks in bird migration? The relative importance of vigilance and fuel load. *J Theor Biol* 231:223–227
- Lind J, Fransson T, Jakobsson S, Kullberg C (1999) Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behav Ecol Sociobiol* 46:65–70
- Lind J, Jakobsson S (2001) Body building and concurrent mass loss: flight adaptations in tree sparrows. *Proc R Soc Lond B* 268:1915–1919
- Lindström Å (1989) Finch flock size and risk of hawk predation at a migratory stopover site. *Auk* 106:225–232
- Lindström Å (1990) The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. *Behav Ecol* 1:102–105
- Lindström Å, Kvist A, Piersma T, Dekinga A, Dietz MW (2000) Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. *J Exp Biol* 203:913–919
- Lindström Å, Rosén M (2002) The cost of avian winter stores: intra-individual variation in basal metabolic rate of a wintering passerine, the greenfinch *Carduelis chloris*. *Avian Sci* 2:139–144
- Moore FR (1994) Resumption of feeding under risk of predation: effect of migratory condition. *Anim Behav* 48:975–977
- Peacor SD, Werner EE (2001) The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc Natl Acad Sci* 98:3904–3908
- Pérez-Tris J, Díaz JA, Tellería JL (2004) The loss of body mass under risk of predation: cost of anti-predatory behaviour or adaptive fit-for-escape? *Anim Behav* 67:511–521
- Piersma T, Koolhaas A, Jukema J (2003) Seasonal body mass changes in Eurasian golden plovers *Pluvialis apricaria* staging in the Netherlands: decline in late autumn mass peak correlates with increase in raptor numbers. *Ibis* 145:565–571
- Pravosudov VV, Grubb TC Jr (1998) Management of fat reserves in tufted titmice *Baeolophus bicolor* in relation to risk of predation. *Anim Behav* 56:49–54
- Schmaljohann H, Dierschke V (2005) Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. *J Anim Ecol* 74:131–138
- Schwarzkopf L, Shine R (1992) Costs of reproduction in lizards: escape tactics and susceptibility to predation. *Behav Ecol Sociobiol* 31:17–25
- Sih A (1986) Antipredator responses and the perception of danger by mosquito larvae. *Ecology* 67:434–441

- Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J Anim Ecol* 71:296–308
- van der Veen IT (1999) Effects of predation risk on diurnal mass dynamics and foraging routines of yellowhammers (*Emberiza citrinella*). *Behav Ecol* 10:545–551
- Whitfield DP (2003) Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *J Avian Biol* 34:163–169
- Wisenden BD, Cline A, Sparkes TC (1999) Survival benefit to antipredator behavior in the amphipod *Gammarus minus* (Crustacea: Amphipoda) in response to injury-released chemical cues from conspecifics and heterospecifics. *Ethology* 105:407–414
- Ydenberg RC, Butler RW, Lank DB, Guglielmo CG, Lemon M, Wolf N (2002) Trade-offs, condition dependence and stopover site selection by migrating sandpipers. *J Avian Biol* 33:47–55
- Ydenberg RC, Butler RW, Lank DB, Smith BD, Ireland J (2004) Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. *Proc R Soc Lond B* 271:1263–1269
- Alerstam T, Lindström A (1990) Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner B (ed) *Bird migration: the physiology and ecophysiology*. Springer, Berlin Heidelberg New York, 331–351
- Hedenström A, Alerstam T (1997) Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *J Theor Biol* 189:227–234