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Letter

Danger management and the seasonal adjustment of migratory speed by sandpipers

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The behavior of migrating birds is governed by time-, energy- and danger-minimizing strategies. The adjustment of migration speed (i.e. the rate at which distance is covered during a migration) is a behavioral tactic that might contribute to these strategic goals. Shorter stopovers and greater fuel loads increase migration speed, but both require more intensive foraging at stopovers, making migrants more vulnerable to predators. A simple numerical model shows how seasonal alterations in migration speed can lower the exposure of western sandpipers to peregrine falcons, their most important predator. The 'caution–speed–caution' pattern of higher migration speed in the mid-passage period, observed in earlier work, requires that the intensive foraging necessary heightens vulnerability, and that migrants are exposed to both migrant predators as well as predators resident at migratory stopovers.

Keywords: danger minimizing, migration, migration speed

Introduction

The term 'migration speed' or 'migratory speed' refers to the rate of travel while on migration, including the time spent at stopovers (Alerstam and Lindström 1990). The review of long-distance migration evolution by Alerstam et al. (2003, p. 252) stated 'If and how birds in the wild adjust their fuel levels and ... migration speed when exposed to predator attacks remains to be shown...'. Several earlier papers had considered the effects of danger on aspects of migratory behavior (Lindström 1990, Bednekoff and Houston 1994, Fransson and Weber 1997, Dierschke 1998, 2003, Ydenberg et al. 2002), and much subsequent work was motivated by this challenge (Schmaljohann and Dierschke 2005, Lind and Cresswell 2006, Duijns et al. 2009, Bauer et al. 2010, Jonker et al. 2010, Lank et al. 2017, Bracis et al. 2018).

Some of these papers consider stopover duration or fuel level, but so far as we are aware, none explicitly considers whether and how migratory speed is adjusted in relation to predation danger. Most of the time on migration is spent at stopovers (> 85% for many bird species), during which migrants forage to replenish body stores of fats and other nutrients (together 'fuel') that power migratory flights. High intensity foraging has a strong influence on migratory speed because it increases the rate of fueling



which shortens the stopover time required to reach a given fuel load, or increases the fuel load attained in a given stopover time (Lindström et al. 2019; see also Schmaljohann and Both 2017) and thus increases the range. Investigating migration speed requires consideration of the foraging intensity at stopover sites.

Western sandpipers *Calidris mauri* migrate southward after breeding in coastal Alaska, and travel 5000–10 000 km to nonbreeding areas from California to Péru, and throughout the Gulf of Mexico and the Caribbean. Alerstam and Lindström's (1990) migratory speed formula predicts that sandpipers could migrate at speeds as high as 400 km d⁻¹ (see Fig. 4 in Hope et al. 2011). The formula contains parameters f (fuel load, expressed as a proportion of lean body mass) and k (daily rate of change in f), allowing calculation of how adjustments in foraging intensity (k) and stopover duration (f/k) affect migratory speed. The faster fueling required to power migratory speed (Lindström et al. 2019) is attained by more intense foraging, lowering vigilance, extending foraging time, foraging in smaller flocks (fewer competitors but less safety), in places with higher food density (but greater danger), or some combination of these behaviors. Beauchamp (2010, 2015) has documented the behavior of southbound semipalmated sandpipers *Calidris pusilla* in relation to these and other factors.

Falcons are the most important predators of sandpipers, and are also migratory. Of the estimated ~11 000 pairs of peregrine falcons *Falco peregrinus* historically present in North America (Cade and Burnham 2003), 75% or more bred north of 55° and migrated southward to lower temperate and tropical latitudes. The southward passage of peregrines over any location occurs over approximately two months, rising to a peak and then falling ('waveform'; Worcester and Ydenberg 2008). In addition to these migrant predators, there are also breeding peregrines at sites throughout the continent, especially in important stopover regions for shorebirds like the Bay of Fundy and mid-Atlantic coast (Dekker et al. 2011, Watts et al. 2015).

In contrast to sandpipers which alternate stopover periods of days or weeks with long flights, peregrines cover about ~200 km (see Lank et al. 2003 for summary of the evidence) on most migration days. They often use low-energy soaring flight, hunt every day and rarely fly or hunt at night. We presume that this suite of migration traits limits the ability of peregrines to increase migratory speed.

Ydenberg et al. (2007) argue that the steadily advancing 'falcon front' exerts an important influence on avian migration. They consider whether traits such the timing and routing of migration could help avoid this transient high danger zone, and ask how they could be adjusted (behaviorally, or by selection) to increase safety. Here we ask whether adjustments in migratory speed might also help migrant prey avoid predators.

As viewed from a stopover site during southward migration, western sandpipers flow by more-or-less steadily over the course of about ten weeks, with adults preceding

juveniles by about a month. The 'caution–speed–caution' hypothesis (Fig. 2 in Hope et al. 2011 gives a schematic presentation) holds that migratory speed should 1) be low for early migrants far ahead of the wave of migratory peregrines; 2) high for migrants just ahead of the wave of predators; and 3) low for late migrants under and behind the falcon front. Hope et al. (2011) reasoned that higher migratory speed allows the distance from the approaching 'falcon front' to be maintained or even increased, but requires intensive foraging which increases vulnerability to any predators already at stopover sites. Their hypothesis was developed verbally, and here we present a simple numerical analysis that seeks to clarify the logic and to make clear the required assumptions.

Our analysis considers a simple five stopover, 5000 km migration. We define the 'start date' of a migration as the first day at the first stopover site (expressed as day-of-year, e.g. d-o-y 172 = 21 June). At each of the five stopovers, migrants spend either four, three or two days loading fuel, and then make a 1000 km flight to the next site, requiring one day to complete this flight. The flight from the final stopover takes migrants to the non-breeding area. With four days stopovers, sandpipers advance 1000 km each five days, giving a migratory speed of 200 km d⁻¹. A total of 20 stopover days with low foraging intensity is required. Shorter stopovers raise sandpiper migratory speed to 250 km d⁻¹ (with three days stopovers; 15 stopover days in total; medium foraging intensity) or 333 km d⁻¹ (two days stopovers; 10 stopover days; high foraging intensity). Higher migratory speed reduces the number of stopover days, but the intensive foraging required makes migrants more vulnerable to predators during those stopovers. This trade-off is at the heart of this analysis (see also Weber et al. 1998). We develop a discrete numerical model to highlight in a simple way basic features of the interaction between migrating prey and their predators.

Sandpipers at stopover sites are exposed not only to migrant peregrines, but also to any predators resident at those sites, including breeding peregrines (Dekker et al. 2011). The presence of resident predators is constant throughout the migratory period, but the abundance of migratory peregrines rises and falls seasonally, and is described by the migratory peregrine exposure index, shown in Fig. 1. This wave or 'falcon front' progresses southward at 200 km d⁻¹, with the peak at subsequent stopover sites later in direct relation to the extra distance. Sandpiper migrations with four days stopovers (plus the day required for the flight) have a migration speed of 200 km d⁻¹ (equivalent to peregrine migratory speed) and thus maintain a migrant's position with respect to the falcon front. Shorter stopovers edge migrants ahead, as shown in Fig. 2.

The model chooses for each start date the migratory speed (200, 250 or 333 km d⁻¹) that maximizes expected migratory survival. The migration schedule is fixed (stopovers of two, three or four days followed by a day's flight) and so the dates at each of the stopovers are known. The expected migratory survival is estimated as the product of survival over all stopover days. Daily survival at each stopover is determined by

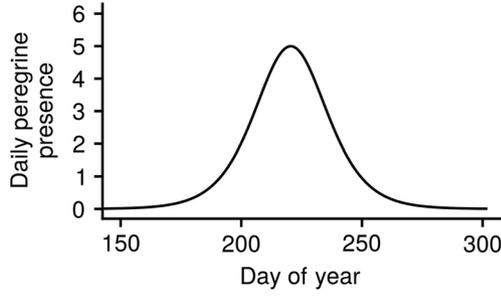


Figure 1. The daily presence during passage of migratory peregrines at any stopover follows a waveform derived from cumulative southward passage (Worcester and Ydenberg 2008), here with asymptote equal to 220, and the rate parameter equal to 0.10 (based on Lank et al. 2003, Hope 2018). Shown here is the value of the migratory peregrine index on day-of-year t at the first ($i=1$). The wave moves southward at 200 km d⁻¹, so that the migratory peregrine index on day t at the next stopover site 1000 km distant, $L_{i+1,t}$ is equal to $L_{i,t-5}$. The value of the resident predator index has a positive value of 0–5, and is constant at all stopovers and days in any run of the model.

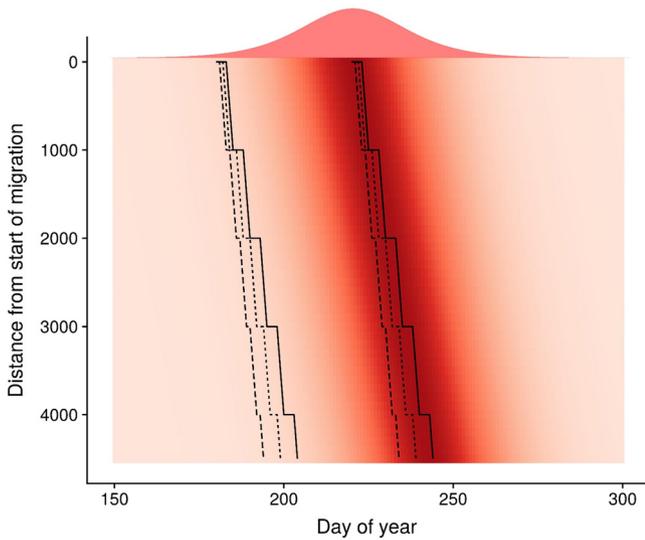


Figure 2. Southward progression of peregrine and western sandpiper migrations. The passage of peregrines over the first stopover (shown in Fig. 2) is portrayed along the top edge of the figure, with its steady southward track at 200 km d⁻¹ indicated by the heat-shaded diagonal. The southward tracks of western sandpipers initiating migration on d-o-y 180 (ahead of peak peregrine passage) or d-o-y 220 (peak peregrine passage) and migrating at 200, 250 and 333 km d⁻¹ are indicated by the stepped solid, dotted and dashed lines, respectively. Migration at 200 km d⁻¹ (the solid line) maintains a sandpiper’s position wrt to peregrine passage, while higher migration speeds (the dotted and dashed lines) are slightly steeper than the peregrine diagonal and hence advance more quickly. The gain over the entire migration is five days (at 250 km d⁻¹) or 10 d (at 333 km d⁻¹). Exposure to migrant peregrines is affected hardly at all for early migrants, but the total exposure is reduced substantially for those migrating during peak peregrine passage.

the predator exposure index, which is the sum of the migratory peregrine index on that day ($L_{i,t}$; Fig. 1) and the resident predator index R , described below.

The extra vulnerability that results from more intense foraging is accounted for by a factor multiplying the predator exposure index, which heightens mortality and thus lowers survival. The expected daily survival on day t (day-of-year) at stopover i ($i = 1, 2, 3, 4, 5$) is

$$S_{i,t} = (1 - \mu(L_{i,t} + R))V_s \quad (1)$$

where $L_{i,t}$ is the migratory peregrine index as described in Fig. 1; R is the resident predator index (in any model run assumed identical on all days and at all stopover sites); V_s is the vulnerability factor with migratory speed s ($s=200, 250$ or 333 km d⁻¹); and μ is a scaling factor to keep survival between 0 and 1.

The model does not consider possible additional effects on fitness of fast or slow migration (e.g. carry-over due to high or low energy expenditure), or of arrival timing on non-breeding areas. We recognize that these factors may have fitness consequences, but our purpose here is to analyze how the danger to survival posed by migratory and resident predators at stopovers interacts with foraging costs and the start date to affect migratory speed. Also implicit is the assumption that survival is higher on nonbreeding areas than at stopover sites. Were this not the case there would be no advantage to continuing migration beyond the stopover site at which this was no longer true.

Results

With no foraging costs ($V_{200}=V_{250}=V_{333}=1$), expected survival is always maximized by the highest migratory speed. The reason is that higher speed reduces the number of stopover days (which is when migrants are exposed to predators), and without foraging costs there is no reason to migrate slowly. Nor does an across-the-board increase in the cost of intensive foraging ($V_{200}=V_{250}=V_{333}>1$) alter this: migrants travel at high migratory speed if there is no extra cost to more intensive foraging.

Intra-seasonal variation in migratory speed requires that the cost of foraging increases with intensity ($V_{200}<V_{250}<V_{333}$). Figure 3 shows the basic patterns that arise with various combinations of these costs. In the absence of resident predators ($R=0$; Fig. 3A), migratory speed shifts abruptly from high speed for early migrants to lower speed for later migrants under almost all combinations. Seasonal patterns resembling the ‘caution–speed–caution’ pattern predicted by Hope et al.’s (2011, 2014) hypothesis appear with the addition of even a low number of resident predators ($R=0.1$; Fig. 3B). The patterns is robust and is found in a large region of the parameter space (with $V_{250} \geq 1.5$, and $2.0 \leq V_{333} \leq 2.9$).

The abundance of resident and migratory predators both affect the migratory speed measured at stopover sites, but

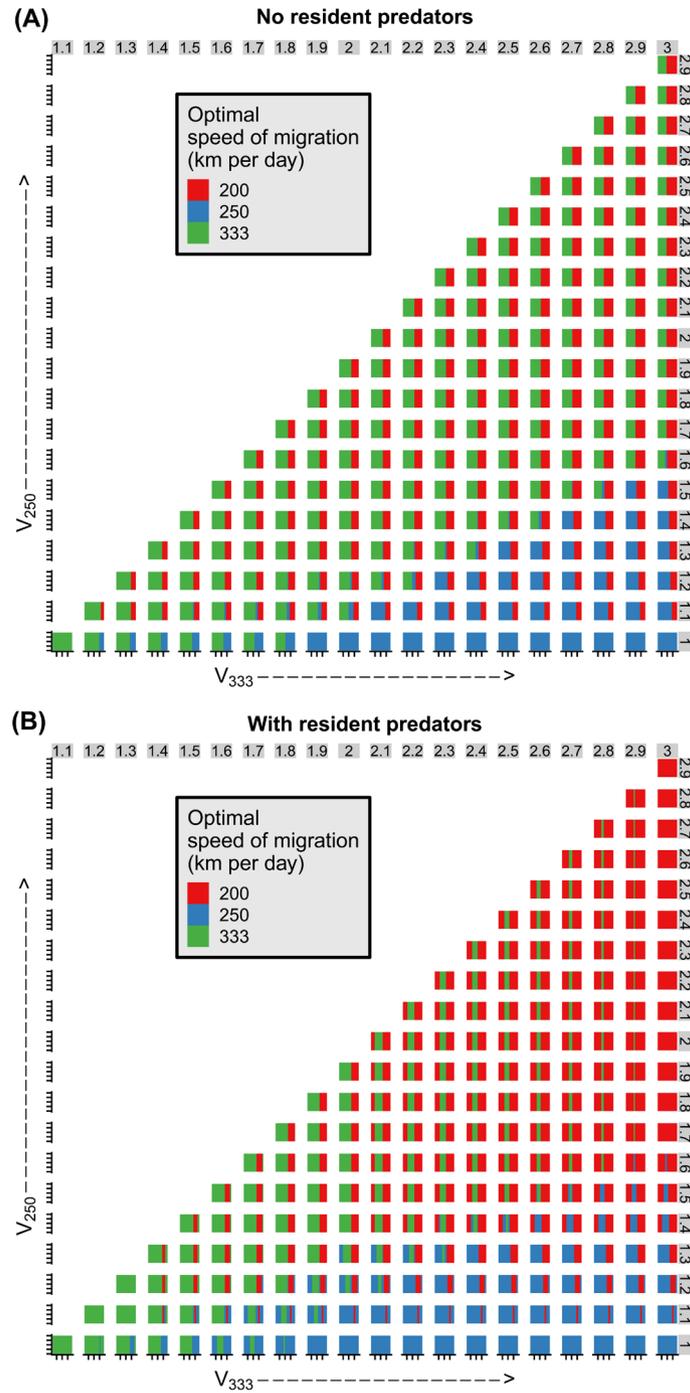


Figure 3. Seasonal migratory speed patterns in relation to the costs of intense foraging. The axes show the vulnerability factors V_{250} (along the x-axis) and V_{333} (along the y-axis), both expressed relative to V_{200} , which is set to 1.0. We assume $V_{200} < V_{250} < V_{333}$, so results are shown below the diagonal only (i.e. where $V_{250} < V_{333}$). Each sub-panel represents an entire passage period for one combination of V_{250} and V_{333} , with d-o-y along its x-axis and colour-coding to indicate the survival-maximizing migration speed of sandpipers initiating migration on each d-o-y (red – 200 km d⁻¹; blue – 250 km d⁻¹; green – 333 km d⁻¹). With no resident predators (upper panel (A)), migratory speed shifts abruptly from high (green) to low (red or blue) under almost all circumstances. With resident predators present ($R=0.1$; lower panel (B)) the ‘caution–speed–caution’ pattern predicted by Hope et al. (2011, 2014) emerges in a broad region of parameter space, shown by a red field with a green or blue stripe in the mid-region.

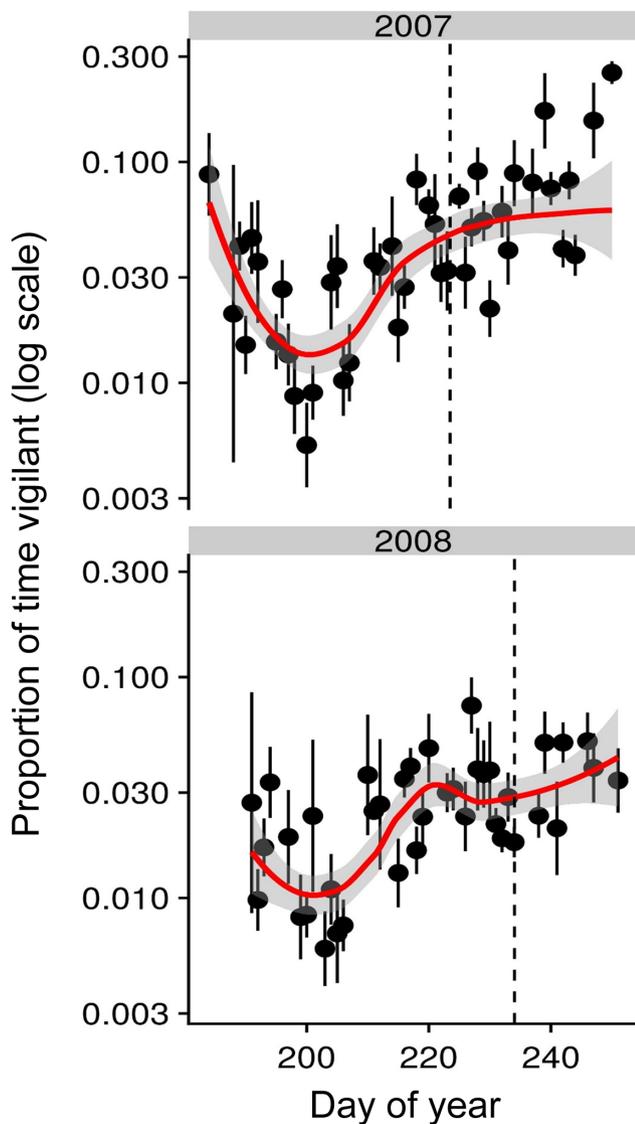


Figure 4. Vigilance levels (proportion of time; note log scale) of foraging western sandpipers during southward migration, measured in 2007 and 2008 on the Fraser River estuary in southwest British Columbia (from Hope et al. 2014, see their Fig. 1). Peak peregrine passage in these years fell on d-o-y 215 (2007) and d-o-y 231 (2008). In both years vigilance falls steeply ahead of peak peregrine passage (indicated by vertical line), and rises as the peak passage date approaches, consistent with the caution–speed–caution hypothesis.

in opposite directions. With baseline parameters ($\mu=800$, $R=0.1$, $V_{200}=1.0$, $V_{250}=1.4$, $V_{333}=2.5$) the mean daily migration speed observed between d-o-y 170 and 260 (enclosing ~98% of passage) at the first stopover site is 240 km d^{-1} . This falls as resident predators increase, to 221 km d^{-1} with the value of R set to 1.0, and 207 km d^{-1} with the value of R set to 5.0. Increasing the number of migratory predators has the opposite effect. With the same set of baseline parameters, migratory speed rises from 240 km d^{-1} with the value of L set to 200, to 245 km d^{-1} with the value of L set to 300, and to 254 km d^{-1} with the value of L set to 700.

Discussion

This numerical analysis clarifies and supports the basic logic of the caution–speed–caution hypothesis proposed by Hope et al. (2011, 2014). So long as the costs (in terms of increased vulnerability to predators) increase with foraging intensity, southbound migrants can elevate migratory survival by altering migratory speed contingent on the start date. With no resident predators, early-departing migrants have high migratory speed, which drops abruptly to lower migratory speed after a threshold date. This pattern is greatly altered when there is even a small presence of resident predators at stopover sites: now early and late migrants are predicted to migrate slowly, while those setting out on intermediate dates migrate at higher speed. Cresswell and Quinn (2013) also found that the presence of two different predators (itinerant peregrines and resident sparrowhawks *Accipiter nisus* altered the nature of the predator–prey interaction).

Quantitative predictions depend on the exact peregrine exposure index and vulnerability factor values used in the calculations, but the basic pattern of a peak in migratory speed ahead of peak peregrine passage is maintained under a broad range of parameter values. Nor does this basic result depend on assumptions about the length of the migration, or of each migratory leg. Intra-seasonal changes in migration speed arise as a consequence of the assumptions 1) that there is a distinct peregrine passage period; 2) that sandpipers are able to attain migratory speeds well above those of peregrines; 3) that resident predators are present at stopover sites; 4) that the intense foraging necessary to raise the fuel loading rate and so shorten stopover duration has costs; and 5) that sandpiper (southward) migratory behavior has been selected to maximize survival.

Weber et al. (1998) developed a dynamic state variable model to examine how migrants should adjust foraging rate and departure fuel load during a four-stopover 2000 km (northward) migration. These behavioral adjustments are analogous to foraging intensity (k) and stopover duration (f/k) as used here, and although not expressed as such in their results, presumably lead to changes in migration speed. Their model is more general and flexible than that presented here. It includes predation risks both of acquiring and maintaining fuel loads (we consider only the former), and considers stochasticity in foraging gain. It allows foraging intensity to vary in the course of each of the four stopovers, allows migrants to skip stopover sites, and incorporates fitness effects on arrival timing. It analyzes the effects of all these factors on migration itineraries. But it does not incorporate the main factor we consider here, namely the interaction with migratory predators. It could presumably be modified to do so.

Do other maximization criteria considered in the migration literature predict seasonal changes in behavioral patterns similar to that predicted here? Theoretically, the ‘caution–speed–caution’ pattern could be generated by a mid-passage period peak in food availability on stopover sites, as this would raise the migratory speed of both time- and energy-minimizing migrants (Weber et al. 1998). It is

widely assumed that shorebirds time passage to match peak food availability at stopovers, so a mid-passage peak in migratory speed might also be predicted by these criteria. Unfortunately, there are few reports of seasonal variation in food availability to support a good assessment of how general this phenomenon might be. Lank et al. (2003) consider this point in more detail. They also report data showing that at a well-studied western sandpiper stopover site, food density increases throughout the southward passage period.

Several features of the theory developed here lend themselves to empirical testing. Better measures of migratory speed are becoming possible (Duijns et al. 2019) as tracking devices improve; this will enable descriptions of intra-seasonal patterns to be compiled – though interpretation of ‘migration speed’ (Lindström et al. 2019) remains an issue. In addition to direct measures of migratory speed, measures of behavior supporting foraging intensity (for shorebirds including vigilance, site choice, foraging rate, flock size, feeding distance from cover, escape distance) should show similar patterns. The behaviour at stopovers of southbound migrant western (Hope et al. 2014; see also Hope 2018) and semipalmated sandpipers (Hope et al. 2011) for example, shows marked intraseasonal changes in stopover behavior. Figure 4 shows one example consistent with changes in migratory speed predicted by the caution–speed–caution hypothesis.

The most unanticipated result of the model is that migratory and resident predators have contrasting effects on migration speed, with migratory predators favoring higher migratory speed, while resident predators favor lower migratory speed. Hence, situations in which migrants face primarily resident versus migrant predators should show different patterns. In fact, it is the relative abundance of these predator types that is critical. In the simple model developed here the resident predator index is identical throughout passage at all stopovers and hence applies to the entire flyway, but in reality the value is likely to differ between stopover sites. Details of behaviour will differ depending not only on site-specific attributes (predators resident at that site), but on conditions elsewhere (migratory predator abundance). The timing of predator migration relative to that of the prey should also have a measurable influence, with greater passage overlap (Lehikoinen 2011) increasing the influence of migratory predators. In summary, seasonal adjustments in migratory speed by prey may be general tactical traits. The essence is the degree to which more intense foraging reduces exposure to migrant predators at subsequent stopovers in relation to the extra exposure to resident predators at the current stopover.

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