Point-of-View

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Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants

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Raptors have long been known to prey on avian migrants (Rudebeck 1950, 1951, Dekker 1980), and several studies estimate significant mortality rates for migrants (Lindström 1989, Kerlinger 1989, Moore et al. 1990, Sillett and Holmes 2002). These findings amply justify Alerstam and Lindström's (1990) identification of safety as one of the prime selective forces shaping the evolution of avian migration strategies and behaviour. However, as shown by a survey of recent volumes on the ecology and evolution of avian migration, safety has garnered much less interest from ecologists compared to that paid to time and energy, the other selective factors identified by Alerstam and Lindström. Several contributions in 'Stopover ecology of Nearctic-Neotropical Migrants' (Moore 2000) briefly consider predation risk, but only one chapter of 17 (by Moore et al. 1995) in 'Ecology and Management of Neotropical Migratory Birds' (Martin and Finch 1995) even mentions predators. Neither 'The Ecology of Migrant Birds' (Rappole 1995) nor the edited volume 'Birds of two worlds: the ecology and evolution of migration' (Greenberg and Marra 2005) devote any attention to the effects of predators on migrants, though one chapter in the latter documents what is known of raptor migrations. That things may be starting to change is evidenced by the inclusion of a paper directly addressing this topic (Lind and Cresswell 2006) in the most recent symposium published on migration issues, in the J. Orn., as well as by the publication of several field experiments (Schmaljohann and Dierschke 2004, Pomeroy et al. 2006).

Here we argue that features of migration such as timing and routing are strongly affected by safety concerns, and that careful consideration of such can illuminate aspects of migratory ecology. Phenomena such as bad weather may also threaten migrant safety, but our interest here is limited to predators. Our thesis is that both density-mediated and trait-mediated effects (see Lind and Cresswell 2005) have profound and pervasive influences on the evolution of avian migration, with the latter being especially significant. We consider a number of continental-scale migratory phenomena and explain how, in contrast to existing explanatory hypotheses, these can be viewed as tactics to increase safety.

The predator landscape

We use the idea of a 'predator landscape' to refer the occurrence of shifting danger along migratory flyways (*sensu* Butler et al. 2003). On the predator landscape, the presence of non-migratory predators creates the background level of danger. Of special interest here, however, are the large spatial and temporal variations generated by the movements of migratory predators that overlay this background. Migrants may be hunted by a variety of predators including gulls and owls (see Alerstam 1990, pp. 343–350), but their most important predators are unquestionably falcons and accipiters. Falcons, notably peregrines *Falco peregrinus*, but also merlins *Falco colombarius* and hobbies *Falco subbuteo* are especially migratory. As a group, accipiters are less migratory (Bildstein and Zalles 2005), but some have long migrations (e.g. Levant sparrowhawk *Accipiter brevipes*), and others (e.g. sharp-shinned hawk *Accipiter striatus*; Mueller and Berger 1967) are partial migrants.

Raptor migrations are generally broad-front phenomena (Bednarz and Kerlinger 1989), though they may concentrate in some places along mountain ranges and coastlines, as well as at locations for long open-water crossings (see Heintzelman 1975). Southward passage at a particular location continues over one to two months, usually with a distinct peak (e.g. Heintzelman 1975). Unlike larger raptors, which migrate largely using energy-efficient soaring and gliding, falcons and accipiters use much powered flight, and must capture prey regularly while on migration (e.g. Hunt et al. 1975, Wiedner et al. 1992). They therefore pose a hazard that rises as their numbers build during migration and moves along flyways with them, creating a dynamic landscape that from the viewpoint of potential prey has dangerous 'peaks' and safer 'valleys'.

On the "Transamerican Flyway" (terminology from Bildstein and Zalles 2005), some five million raptors migrate each autumn, generally following the north-south orientation of the Americas. Peregrines, merlins and ospreys may make long open water crossings, but most species avoid these and are funneled along the Gulf coast to Central America, and to South America through the Panamanian isthmus. Raptors on the "Western European–West African Flyway" follow the northeast–southwest axis of the continent (e.g. Ganusevich et al. 2004), sweeping out of Russia and Scandinavia to cross to Africa at the Strait of Gibraltar and the Dardanelles (Bildstein and Zalles 2005 report 200,000 birds). Additionally, Eleonora's falcon *Falco eleonorae* and the sooty falcon *Falco concolor* breed in late summer across the Mediterranean and mid-east, where they exploit the fall migration of small birds. (The absence of analogous species in the Americas is an interesting conundrum; see Walter 1979). In both Europe and North America, a sedentary or partially-migratory race of peregrines flanks the main flyway on the northwest (in the British Isles, and in the Pacific northwest), and breeds earlier than its continental conspecifics.

These raptor species and their movements combine to create predator landscapes with defining characteristics on all the major flyways. The main feature on each is the southward movement and concentration of accipiters and falcons following their dispersed breeding period (see Fig. 1). In North America the direction is southwards, while in Europe migration is directed to

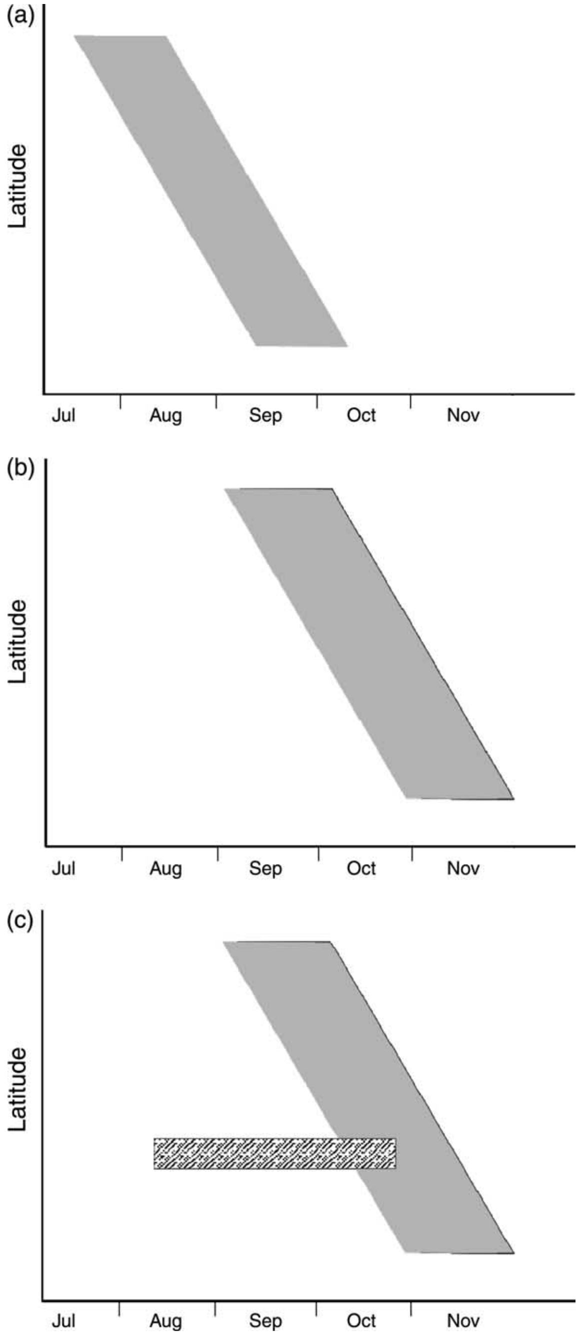

Fig. 1. Schematic representation of the predator landscape of (a) the western portion of the Transamerican Flyway; (b) the eastern portion of the Transamerican Flyway, and (c) the Western European–West African Flyway. Shaded areas show the main concentrations of raptors preying on migrants. The western portion of the Transamerican Flyway differs from the eastern portion in that the main body of raptor migration takes place 4–6 weeks earlier. The Western European–West African Flyway differs from the Transamerican Flyway in presence of Eleonora's falcon and other raptors specialized on autumn migrants (hatched bar in panel c), which creates a hazard that New World migrants do not face.

Fig. 1 (*Continued*)

the southwest (e.g. Ganusevich et al. 2004). On the eastern portion of the Transamerican Flyway, and on the Western European–West African Flyway, this occurs from September to November, with a marked peak during October. On the Western portion of the Transamerican Flyway raptor numbers begin building in August, as much as six weeks earlier than on the east coast. Lank et al. (2003; their Fig. 3) illustrate the annual rhythm in peregrine numbers at a coastal site in southwest British Columbia. Here sightings rise rapidly in mid-August, compared with the early October peak of peregrine passage at Hawk Mountain, Pennsylvania (Heintzelman 1975), which lies only a few degrees of latitude further south. A compilation of raptor passage data from sites across the continent reveals that the band of southbound peregrine migration is oriented southwest – northeast across the continent (Worcester and Ydenberg unpubl. data; see also Lank et al. 2003).

In Europe, a potentially similar influence is negated by the geography of the continent. Further, the presence of Eleonora's and sooty falcons creates a hazard not shared with the Transamerican Flyway. These birds breed in August and September during the peak of migration from Europe (see Walter 1979, p. 202). These flyway-scale differences are summarized in Fig. 1. We can now begin to examine how the predator landscape and the differences between flyways have affected migratory ecology and evolution.

North-south route differences

Many migrants follow different north- and southbound routes. On the Transamerican Flyway some songbirds cross the Gulf of Mexico from the Yucatan peninsula when northbound, for example, but fly a route around the Gulf when southbound (Gauthreaux 1999). Among birds crossing the Caribbean, southbound routes are typically shifted eastward relative to the northbound crossing, creating so-called 'elliptical' migrations (Rappole 1995). Other species make a long southbound transoceanic crossing from the Atlantic seaboard to South America, but fly up the western Gulf coast and Mississippi Valley when northbound.

These route differences are widely attributed to the influence of prevailing wind patterns (e.g. Moore et al. 1995, Williams and Webb 1996), the idea being that migration routes evolve readily along routes with favorable winds. Generally, easterlies prevail over latitudes of the southern continental USA. and the Caribbean, while westerlies prevail at higher latitudes, which would favor an eastward shift of the southbound route. We do not doubt that following winds provide energetic advantages for migrants, or that migrants are careful to fly with tailwinds when possible. Some long-distance flights might even be difficult or impossible without assisting tailwinds (Butler et al. 1997, Green 2004). But we suggest that these differing routes may also have previously unrecognized safety features that favor their use.

To examine this hypothesis, it is instructive to compute the time and energy costs of the possible alternative routes that migrants could fly. An analysis of a north-south route difference of western sandpipers *Calidris mauri* provides an illustrative example. When northbound these birds fly along the British Columbia-Alaskan coastline (i.e. circum-Gulf of Alaska), but when southbound they cross over the Gulf of Alaska. Initially, it was felt that this pattern was due to the influence of prevailing winds (Butler et al. 1996), but an analysis comparing the estimated energy and time costs of these alternative routes found that trans-Gulf flights were cheaper and faster both north- and southbound (Lank et al. 2003; see their Table 2).

Lank et al. (2003) suggested that safety considerations could explain the difference, hypothesizing that high predator presence in spring in the region from which northbound western sandpipers would have to launch a Gulf of Alaska crossing (southwest British Columbia) makes the requisite heavy fuel load too costly in survival terms, whereas the southwest coast of Alaska provides a safe staging area for the southbound crossing. The short legs of the coastal route (900–1100 km) each require a smaller fuel load than is needed for the trans-Gulf of Alaska crossing (~2900 km), though the total distance (~3300 km) is greater, and the total amount of fuel larger. Safety considerations may thus alter the fueling schedule, making short 'hops' or medium 'skips' preferable to long 'jumps'.

Safety may affect the choice of route even in the absence of fueling considerations. For migrants on the Transamerican flyway, an eastward shift of the southbound autumn route relative to the northbound spring route could provide a safety advantage as shown in Fig. 2. Raptor migration occurs later toward the eastern part of the continent, so a south-easterly flight would under some circumstances put autumn migrants further ahead of the advancing predator front than would a southerly flight of the same distance. Fall migrants at many locations in the continental United States show exactly such a south-easterly bearing (Moore et al. 1995; see their Fig. 5–3), traditionally explained by wind patterns. We can use observations made at places where wind directions are variable, or prevail in directions opposite to that of migration, to discriminate between the wind and safety hypotheses. In the mid-west, for example, wind directions are diverse, there are no coastlines or mountains to deflect migrants, yet the south-easterly bearing of migrants is strongly evident everywhere. Interestingly, monarch butterfly *Danaus plexippus* migration routes to destinations in north-eastern Mexico from these same places do not show

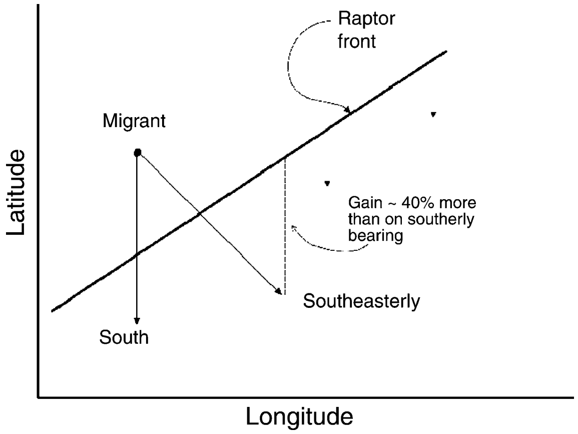

Fig. 2. How a southeast bearing gives Transamerican migrants extra safety. Raptor southward migration shows a strong west-east gradient across North America, with peak passage in the west a month or six weeks earlier than in the east (from Lank et al. 2003). For peregrines the front moves southward at ~170 km d^{-1} (Fuller et al. 1998). Travel for migrants is assumed relatively safe ahead of the predator wave front, but hazardous underneath it. With a southeasterly bearing, a migrant gains about 40% more distance on the predator front for a given flight distance than with a southerly bearing.

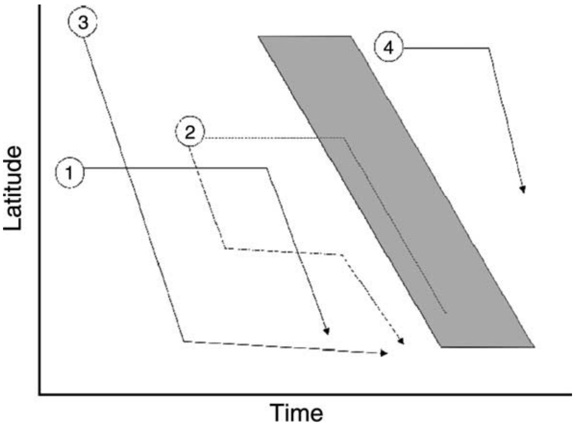

Fig. 3. Primary molt and migration. Raptor migration is indicated by the shaded area. For migrants, molt is indicated by horizontal lines, migration by sloped lines. Schedule 1 is pre-migratory or 'summer' molt that takes before the passage of raptors. Schedule 2 illustrates how molt-migration could be advantageous. In the example shown, there is not enough time to complete molt (dotted line) at the breeding location before the arrival of raptors, but a partial migration allows enough distance to be gained on the raptor front so that molt can be accomplished before completing migration. Schedule 3 is post-migratory or 'winter' molt, as shown by long-distance migrants like the western sandpiper and reed warbler *Acrocephalus scirpaceus*. On schedule 4 molt is completed prior to migration, but takes place after the passage of raptors. This option is available only at high latitudes (e.g. Pacific dunlin *Calidris alpina pacifica;* see Lank et al. 2003).

these effects (see Alerstam et al. 2003), even though we might expect butterflies to be more strongly influenced by wind than are birds.

Unfortunately, no other comparisons of alternative possible routes have been published, so we cannot yet tell how general this pattern might be. We predict, though: (1) that the routes flown by migrants will not always be found to be cheaper or faster than other possibilities, which would be too dangerous and are hence avoided, and (2) that cases where birds substantially compromise their escape performance by putting on stores for extremely long migration segments will occur predominantly under safer conditions.

Primary molt

The majority of non-migrant avian species molt body and flight feathers immediately following breeding, so-called "summer molt". Migrants show greater variability, and may molt prior to, during, or after southward migration. Phylogenetic analyses of both old and new world taxa (Svensson and Hedenström 1999, Rohwer et al. 2005) indicate that summer molt is the ancestral state, and that deferred molt has multiple independent evolutionary origins. Many hypotheses have been proposed for this, though so far as we are aware only one considers a possible influence of predation danger. Holmgren and Hedenström (1995) developed a dynamic state variable model in which the scheduling of molt is a compromise between the effect of feather quality on breeding success and on winter survival. Their model is able to generate all the known patterns under various parameter value combinations, including molt-migration (i.e. migration interrupted by a molt) as well as biannual molt. They explicitly assume that mortality is elevated during both molt and migration, but their model does not incorporate the predator landscape effects considered here.

Interactions of primary molt schedules (i.e. molting primaries prior to, during, or after migration) with the predator landscape are diagrammed in Fig. 3. For ease of reference, we refer to four basic molt schedules. On Schedule 1 (= "summer molt"), molt immediately follows breeding. Southward migration is therefore undertaken on fresh primaries, which presumably improves migratory ability, aids in crossing barriers like deserts or large bodies of water, and removes the need for further molt upon arrival at the destination. Our main assumption is that molting is dangerous, and we contend that for summer molt to be advantageous, breeding must be completed far enough in advance of raptor migration. We argue that this is the general situation on the eastern portion of the Transamerican

Flyway, where the great majority of neotropical migrants (~95% of species; data along with phylogenetic trees in Rohwer et al. 2005) molt both primaries and body plumage prior to undertaking migration.

On the western portion of the Transamerican Flyway raptor migration occurs much earlier, which puts some species in the situation depicted by Schedule 2 (= "molt migration"). The delay that results from undertaking molt prior to migration is now more hazardous. Accordingly, about half of all western species undertake a molt-migration (Rohwer et al. 2005). Evidence that these are true differences between the ecology of the western and eastern portions of the Transamerican Flyway is provided by painted buntings *Passerina ciris*: Western populations are molt-migrants (Schedule 2), while eastern populations are summer molters (Schedule 1). Rohwer et al. (2005) attribute the high frequency of molt migration to the general aridity of the west and consequent shortage of resources to power the molt. They suggest that many western migrants undertake molt in the Sonoran desert, where the 'Mexican monsoon' provides late summer rains and a flush of food. The predator landscape hypothesis is not incompatible with this idea, but asserts that molt migration's main advantage is to gain enough distance on the predator front so that molt may be completed in relative safety. Norris et al. (2004) documented conditional molt strategies of American redstarts *Setophaga ruticilla* breeding at a site in eastern North America. Most individuals are summer molters, but late breeders (i.e. closer to the arrival of raptors) were more likely to undertake a molt migration, and moreover, the later breeding was completed, the further south molt took place, exactly as Fig. 3 would predict.

Schedule 3 (= "winter molt") can be considered the extreme version of molt-migration, in which molt is not undertaken until migration is complete. In the New World, a variety of species are winter molters, among them western sandpipers (Lank et al. 2003), but no New World songbirds use this strategy (Rohwer et al. 2005). In contrast, winter molt is common among songbirds on the Western European-West African flyway. The predator landscape of the Western European-West African flyway differs from that in the New World due to the presence of fall-breeding falcons across the Mediterranean and Middle East (see Fig. 1c). For some species, a molt prior to migration would delay the Mediterranean crossing molt into the period of peak Eleonora's falcon breeding. Accordingly, this flyway exhibits strong contrasts with in molt patterns with the New World, as detailed for warblers by Svensson and Hedenström (1999). First of all, post-migratory ('winter') molt is prominent, having evolved independently 7–10 times. In a further contrast with western North America, species with molt-migration seem to be almost absent, though Svensson and Hedenström (1999) identify two "split molters", who molt half of flight feathers in summer and half in winter. Finally, all species delay body molt until after migration regardless of where flight feathers are molted (cf. the New World, where body plumage and flight feathers are molted together; Rohwer et al. 2005).

Concluding remarks

Our point-of-view is that the danger generated by raptors and their migrations has had profound and pervasive effects on the evolution of avian migration. We have detailed two examples (north-south route differences, and molt timing), but other aspects of migratory behavior might also be considered in light of safety considerations. For example, Woodrey (2000) details differences between adult and juvenile long-distance migrants. In some species juveniles are later migrants than adults, and therefore face greater predation danger. Migration tactics and even morphology (e.g. wing shape) differing from adults may be advantageous for this reason. One might expect the use of safer tactics by younger birds (e.g. reduce fuel load, use safer habitats), but because these would slow the migration, dangerous tactics (e.g. higher fuel loads, use of more dangerous but better feeding habitats) that speed the migration and reduce the duration of exposure might instead be better. The best tactics will depend on the relative survival costs of the behavior, and the duration of exposure (i.e. cumulative danger).

Several studies may be interpreted to indicate that juveniles adopt the 'fast-migration' option. For example, Dierschke (1998) found that Helgoland (a North Sea stopover site for many southbound migrants) offers excellent feeding opportunities, but is also very dangerous for migrants. Juvenile dunlins *Calidris alpina* frequent Helgoland, whereas adult dunlins avoid it. Dierschke suggested that juveniles are naïve about the danger, and must learn to avoid the site. On the Atlantic and Gulf coasts of North America, southbound adult songbirds are found in higher proportions on inland sites, whereas juveniles predominate on coastal sites, a phenomenon called the 'coastal effect' (see discussion in Rappole 1995). Ralph (1978) suggested that young birds are disoriented, and wind up in coastal habitats by mistake. Rappole et al. (1979) hypothesized that young birds were inferior competitors and were thus excluded from the best habitats by adults. Moore (1999), however, showed that coastal habitats are superior for feeding, but also more dangerous (as was found for dunlins on Helgoland) and suggested that young birds are hungrier and thus take greater chances. These examples suggest that the ultimate reason for the differences in the behavior of adults and juveniles is not the inexperience, recklessness or lower capability of juveniles, but rather lies in the ecology of the situation in which they find themselves. Other aspects of migratory behavior could be examined in analogous ways.

We feel there are several reasons why ecologists have given less attention to safety than to time and energy in studies of migration strategies. Alerstam and Lindström (1990) identified "time-minimizing", "energy-minimizing" and "safety-maximizing" criteria in their inspirational paper (see Houston 1998). They derived testable predictions for the first two criteria using flight mechanical theory, but analogous predictions for safety-maximizing are more elusive. In order to evaluate the relative contributions of time, energy and safety to migratory behavior, clear and testable predictions that contrast with those for other criteria are required.

We feel, however, that the biggest factor leading most ecologists to doubt the importance of safety is that predators do not kill many migrants relative to the total. All the Eleonora's falcons together, for example, catch only a tiny fraction (< 0.05%) of the 5000 million or so migrants crossing the Mediterranean (Alerstam 1990; p 348, based on figures in Walter 1979). But as we have previously elaborated (Lank and Ydenberg 2003), mortality *per se* is not the relevant measure of danger (see also Lind and Cresswell 2005). An analogy can be made with pedestrian safety in a busy city, where crosswalks, traffic lights, barriers, education campaigns, intersection cameras, police vigilance and other measures help to keep the fatality rate low. Clearly, it would be wrong to use the low mortality to argue that cars are not an important factor in pedestrian ecology. In fact, cars are such a threat to pedestrians that these expensive investments are worthwhile.

Analogously, low mortality on migratory flyways cannot be used as evidence against the potential importance of predators. The crux of the issue is whether mortality is low because the danger is low, or because prey individuals are able to employ anti-predation tactics that effectively counter pervasive danger. To answer the question of whether the migratory traits considered here evolved to reduce mortality from predators, we need an assessment of how much higher the mortality would be for individuals that do not undertake these alleged precautionary measures.

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