



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*)

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

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"),(e)-3mt fe(e4ibange) -1.14390i2-0

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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