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Passerine migrants respond to variation in predation risk during stopover

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During travel, migrants may encounter unfamiliar habitats and predators and visit sites for which they lack information on predation risk. Temporary stops during migration permit only limited opportunities to gather information about risk, and other priorities, such as the need to forage, may restrict these opportunities. Under these conditions, the extent to which migrants respond to variations in predation risk is unclear. We studied small passerine birds during migratory stopover to determine whether their behaviour was related to variation in risk of capture by migrating birds of prey. We used two approaches, observational and experimental. Observations revealed that blue-grey gnatcatchers, *Polioptila caerulea*, and American redstarts, *Setophaga ruticilla*, moved deeper into oak shrubs as the number of sharp-shinned hawks, *Accipiter striatus*, at the site increased. Furthermore, blue-grey gnatcatchers moved at slower rates as counts of hawks increased. The experiment revealed that blue-grey gnatcatchers had lower rates of both movement and foraging after exposure to a gliding model hawk. These results provide evidence that predator avoidance remains a priority during migration and that migrants are able to assess risk to some extent during temporary stopover. In addition, the results suggest that predator avoidance behaviour may limit foraging opportunities during stopover by restricting habitat use.

During migration, animals may be exposed to great variation in predation risk over both space and time. This is especially true of birds that migrate in stages separated by periods of stopover. Migrating birds of prey can present an important component of the risk facing other migrant birds (Rudebeck 1950, 1951; Lindström 1989, 1990). Raptors migrate during the same period as their small landbird prey (Aborn 1994) and often concentrate along mountain ridges and shorelines (Heintzelman 1975). These concentrations increase the variation in predation risk among stopover sites. Overlaid on this spatial variation is temporal variation resulting from weather-driven pulses of raptor migration (Allen et al. 1996).

The temporary nature of migratory stopover restricts birds' abilities to assess predation risk. Upon arrival, migrants may have little information concerning predation risk at a site. This is especially true of young birds making their first journey in the autumn. Not only would such individuals stop at sites they have never before visited, but they will also encounter habitats and predators with which they have had no previous experience. The short duration of stopover limits the amount of information that migrants can gather about a site. Competing demands during stopover further restrict migrants' abilities to gather information about risk. At this time, foraging demands may be great in order to deposit the fat needed to fuel long-distance flight and, consequently, birds may accept higher risk during migration than at other times (Metcalfe & Furness 1984; Moore 1994).

Thus, migrants face an unusual combination of factors during stopover that may limit their ability to respond to the variations in risk that they encounter and it is unclear to what extent they actually respond behaviourally to those variations. The purpose of this investigation was to determine whether small landbird migrants react to changes in risk during stopover. We examined the relationship between behaviour and the risk associated with the presence of migrant birds of prey because these predators are a variable and likely significant component of risk during stopover. We used two approaches in our

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investigation. First, we observed the behaviour of foraging birds in relation to the naturally varying abundance of migrant raptors. Second, we experimentally examined the behaviour of birds in response to a simulated encounter with a hawk; that is, to a sudden change in perceived level of predation risk. By combining both approaches we took advantage of the strengths of each, namely, realistic natural conditions (i.e. high external validity; sensu Kamil 1988) for the observational study and control of variables (i.e. high internal validity) in the case of the experiment.

Sih (1987) developed a series of predictions describing the behaviour of animals under predation risk. The first of these is that as risk increases, prey should decrease their exposure. We predicted that migrants would adjust their behaviour in accordance with the risk of predation from raptors in ways that would reduce their exposure to these aerial predators. Specifically, we predicted three behavioural responses from two focal species of foliage-gleaning birds in response to increasing predation risk: (1) they would forage progressively deeper inside protective cover; (2) their rate of movement would decrease; (3) their rate of foraging movements would decrease. Moving deeper into cover would decrease their visibility to hunting raptors and the network of branches would provide physical protection. Movement and foraging are relevant to predator avoidance in two ways. First, birds of prey are attracted to movement when selecting prey (Snyder 1975; Smallwood 1989) and thus, by moving less, prey decrease their likelihood of attack. Second, movement and foraging rates are negatively correlated with vigilance (Powell 1974; Milinski & Heller 1978). Scanning the environment for predators, no matter how briefly accomplished, necessarily requires time, and must therefore decrease the rates of other activities. Consequently, a negative relationship should exist between vigilance and both movement and foraging rates.

METHODS

We conducted this study at Bon Secour National Wildlife Refuge on the coast of Alabama, U.S.A. (30°14′N, 88°00′W). The site was 2 km from the end of a peninsula bordered on one side by the Gulf of Mexico and on other by Mobile Bay. We observed migrants in shrubland habitat where it was relatively easy to follow and observe them. In this habitat, the dominant woody plants were the oak shrubs *Quercus geminata* and *Q. myrtifolia* and the majority of these were less than 3 m tall.

We collected data during September and October 1996–1998. During the autumn migration period, both migrating passerines and raptors can be abundant at the site. Days when migrating birds of prey were numerous were not as common as days when migrating passerines were numerous and this facilitated observation of focal passerines over a range of raptor abundance. We chose two focal passerine species that were abundant and relatively easy to observe: blue-grey gnatcatcher, *Polioptila caerula*, and American redstart, *Setophaga ruticilla*. Both species had a long period of passage through the study site, allowing many potential days of observation.

We observed the two focal species during the first 6 h after sunrise and recorded observations vocally on a microcassette recorder. For both the observational and experimental components of the investigation, we focused on the same three aspects of behaviour. The first of these was the bird's depth in the protective cover of the oak shrubs. Most shrubs branched densely and their leaves were concentrated near the branch ends. We estimated the distance from the bird to the nearest outside edge of the shrub to the nearest 10 cm. During the observational study, we recorded these data once for each bird at the time when a tone first sounded from a wristwatch carried by the observer. Because the watch gave this signal every 30 s throughout the entire time that the observer searched for and watched birds, it could sound at any time within the first 30 s of a particular observation. We operationally defined the remaining two aspects of behaviour as follows: movement rate was the number of perch changes per minute and foraging rate was the number of foraging manoeuvres per minute.

We attempted to collect data on focal birds whenever we encountered them, observing them from a distance of 3–15 m. Although we mist-netted migrants on the site during daily trapping sessions and banded them with U.S. Fish and Wildlife aluminium leg bands, the focal birds were not individually identifiable from a distance, so it was possible for the observer to record data on the same individual more than once. To reduce this possibility, the observer worked systematically across the site in one direction to avoid encountering the same bird more than once. After traversing the entire site, the observer waited 30–60 min before searching again. This allowed time for birds that had been observed to move off the site. Based on our recapture data, we found that most birds moved steadily east away from the tip of the peninsula and few of the birds remained on the site for more than 1 day (only 7.5% of American redstarts and 6.8% of blue-grey gnatcatchers were recaptured). Because of our search protocol and the low recapture rate, we believe that our data contain few if any repeat observations on individual birds.

Estimates of movement and foraging rates can lack precision if they are based on short observations. We sought to minimize this source of variance by estimating how long it was necessary to observe a bird before a stable estimate of these rates could be gained. To do this, we examined long observations (>80 s) of both the blue-grey gnatcatcher ($N = 12$) and American redstart ($N = 10$). For each 5-s increment of an observation, we calculated movement and foraging rates based on the information gathered up to that point. We then plotted these rates against observation time. Values for both rates varied considerably during the early stages of observations, but stabilized later. We examined each plot and subjectively determined when stabilization occurred. We then took the mean stabilization time for each species to be the minimum length for an observation to be included in the analysis. For movement and foraging rates of blue-grey gnatcatchers, this minimum time was 23 s and, for American redstarts, the corresponding values were 18 and 21 s, respectively. These observation times were