Fat Affects Predator-Avoidance Behavior in Gray Catbirds (Dumetella carolinensis) During Migratory Stopover

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FAT AFFECTS PREDATOR-AVOIDANCE BEHAVIOR IN GRAY CATBIRDS (DUMETELLA CAROLINENSIS) DURING MIGRATORY STOPOVER

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ABSTRACT.—During migration, birds may store large quantities of fat to fuel long-distance flight. Because mass affects flight performance, fat migrants should behave with greater caution toward aerial predators than lean migrants. We tested a prediction of this hypothesis, namely, that fat birds will remain motionless longer than lean birds after a simulated encounter with a raptor. We captured Gray Catbirds (Dumetella carolinensis) during fall migration, classified their subcutaneous fat, exposed them to a model hawk, and then recorded the time until their first perch change. To determine whether the birds treated the simulated predator as a threat, we also tested them with a hexagon-shaped model and with no model. The birds remained motionless longer with the hawk model than either of the two other treatments. Fat birds remained motionless longer than lean birds when exposed to the hawk model, but we detected no difference with the other two treatments. These results provide evidence that fat affects the predator-avoidance behavior of Gray Catbirds during migratory stopover. That a difference between fat and lean groups was only apparent with the hawk model treatment suggests that the result is attributable to differences in the flight performance of the two groups rather than simply a difference in motivation to begin foraging. We suggest that fat should influence the behavior of a wide variety of migrant birds, particularly those species that typically carry greater fat reserves or that forage in more exposed situations than the Gray Catbirds we tested. Received 23 December 2004, accepted 12 November 2005.

Key words: Dumetella carolinensis, Gray Catbird, migration, predator avoidance, stopover.

La Grasa Afecta el Comportamiento de Evasión de Depredadores en Dumetella carolinensis durante las Paradas Migratorias

RESUMEN.—Durante la migración, las aves pueden almacenar grandes cantidades de grasa para abastecer los vuelos de larga distancia. Debido a que la masa afecta el desempeño del vuelo, los migrantes gordos deberían comportarse con mayor precaución que los migrantes magros en relación con los depredadores aéreos. Evaluamos la predicción de esta hipótesis de que las aves gordas permanecerán sin moverse por más tiempo que las aves magras luego de un encuentro simulado con una rapaz. Capturamos individuos de la especie Dumetella carolinensis durante la migración otoñal, clasificamos su grasa subcutánea, los expusimos a un modelo de halcón y luego registramos el tiempo hasta que las aves cambiaron de posición. Para determinar si las aves consideraron al modelo del depredador como una amenaza, también evaluamos su reacción frente a un modelo con forma hexagonal y su comportamiento.

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Among the hazards that small birds face during migration is the threat of predation by hawks (Accipitridae) and falcons (Falconidae) (Rudebeck 1950, 1951; Lindström 1989; Moore et al. 1990). Many such birds of prey are themselves migratory, and their seasonal passage can coincide with that of their prey (Aborn 1994). The presence of these migratory raptors may add significantly to the risk of predation experienced by migrating passerines when they stop to forage, often in unfamiliar environments. Although these small birds likely experience marked variation in risk over the course of their journeys, it is possible for them to adjust to it, to some extent, through modification of their behavior. The proximate factors controlling these predator-avoidance behaviors during stopover are not known.

The quantity of fat stores a migrant carries is one factor that potentially affects its predator-avoidance behavior during stopover. Fat is the principal fuel for long-distance flight and, during migration, passerines may store large amounts (Lindström and Alerstam 1992, Lindström and Piersma 1993). Storage of fat increases body mass and consequently alters flight performance (Hedenström 1992, Witter et al. 1994, Metcalfe and Ure 1995, Lee et al. 1996, Veasy et al. 1998). Indeed, variation in take-off abilities of migrants has been linked to variation in the size of their fat stores. For example, Kullberg et al. (1996) determined that, when the fat load of the Blackcap (Sylvia atricapilla) increased from 0% to 60% of lean body mass, angle of climb decreased 32% and take-off velocity decreased 17%. Similarly, Lind et al. (1999) found that migrating European Robins (Erithacus rubecula) with fat loads representing 27% of lean body mass had take-off angles 17% lower than those of European Robins carrying no fat. Such changes in flight performance might increase the vulnerability of fat migrants, as compared with lean ones, to attacks by aerial predators. Thus, it is reasonable to predict that migrants should behave with increasing caution as they deposit increasing quantities of fat.

Another way that fat might influence predator avoidance behavior is by altering a bird’s motivation to forage. Optimality models predict that animals with greater motivation will take greater risks (Krebs 1980), and there are many examples of animals accepting greater predation risks as their risk of starvation increases (see Lima and Dill 1990). For example, Koivula et al. (1995) found that hungry Willow Tits (Poecile montanus) spent less time scanning and less time within protective cover than satiated birds. Similarly, it has been shown that some birds increase foraging at the expense of vigilance when preparing to migrate (Metcalfe and Furness 1984, Moore 1994), which indicates that the demands of migration can increase the priority of foraging in the same way that increasing risk of starvation does. However, if the motivation of migrants to forage declines as they accumulate fat, fat migrants should be more cautious with respect to predation risk than lean migrants. Thus, it is reasonable to predict that migrants will show increasing aversion to predation risk as they deposit greater fat reserves, because of decreases in both motivation to forage and flight performance.

Because of the variability that characterizes both the fat loads carried by migrants and the predation risks they face, fat might be an important factor in the control of behavior during
migratory stopover. The objective of the present study was to determine whether fat affects the predator-avoidance behavior of migrants during stopover. Specifically, we tested the hypothesis that if fat affects behavior, fat migrants will be more averse to predation risk than lean migrants. Others (e.g., Hegner 1985, Waite and Grubb 1987) have interpreted increasing latency to begin movement as a reflection of increasing aversion to predation risk. Likewise, we used latency to begin movement following exposure to a model predator as a measure of risk aversion in a field experiment. We predicted that fat migrants would remain stationary longer than lean migrants because these birds would have relatively lower flight performance and motivation to forage.

**Methods**

We conducted the present study during October 1997 and 1998 at Bon Secour National Wildlife Refuge on the Gulf Coast of Alabama (30°13′48″N, 88°00′08″W). Work focused on behavior of the Gray Catbird (*Dumetella carolinensis*). This species is both abundant and easily captured during migration at this site. Furthermore, Gray Catbirds are attacked by migrant accipiters (D. A. Cimprich pers. obs.), so it is reasonable to expect that their behavior is sensitive to predation risk during stopover. We captured birds in mist nets and banded them to ensure that individuals would not be tested twice if recaptured. One observer (D.A.C.) categorized the visible, subcutaneous fat deposits of each bird according to a six-point, ordinal scale (see Helms and Drury 1960, Moore and Kerlinger 1987), such that those with no fat received a score of 0, whereas those with the greatest quantity of fat received a score of 5. This is a fairly precise method of indexing fat stores for intraspecific comparisons (Krementz and Pendleton 1990, Lindström and Piersma 1993).

For analysis, each Gray Catbird was classified as either “fat” or “lean” on the basis of its fat score. The “lean” group consisted of those with scores of 0 or 1, whereas the “fat” group consisted of those with scores of 2–5.

Because fat scores are somewhat subjective, we present additional description of the “fat” and “lean” groups. First, we compared the mass of the birds. However, comparisons of mass alone may not fully reveal how the groups differ in their abilities to escape predation. Thus, we also compared the wing loading of the two groups, because of its direct effect on aspects of flight performance (Hedenström 1992, Norberg 1995). We determined wing loadings for the Gray Catbirds by using measurements of mass and wing chord (wing length measured from the wrist to the tip of the longest primary). We estimated wing area from wing chord by using a regression model of wing chord on wing area based on measurements of 231 Gray Catbirds captured at the study site in October 1993 ($r^2 = 0.54, P < 0.0001$). Estimates of wing area and measurements of mass then allowed calculation of wing loading. We report wing loading in Newtons m$^{-2}$ (N m$^{-2}$).

It is not clear whether age affects the predator-avoidance behavior of Gray Catbirds, and an examination of this factor was not an objective of the present study. However, to decrease any potential confounding effects of age, we gave each of the two recognizable age groups equal representation within both the fat and lean groups. Both consisted of 42% adults. We used degree of skull pneumatization to determine the age of each Gray Catbird, adult or immature (Pyle 1997).

As a measure of predator-avoidance behavior (i.e., caution or risk aversion), we examined the length of time that Gray Catbirds remained motionless following exposure to a simulated predator. Ceasing movement (“freezing”) can be an effective means of avoiding attack by birds of prey that are attracted by activity (Smallwood 1989), and it is a common tactic employed by small birds (e.g., Gaddis 1980, Koivula et al. 1995). Our experiment involved releasing birds into a brushpile (see below) and exposing them to a “flying” model hawk. A bird remaining stationary within this cover would be somewhat protected from attack, whereas a bird flying from it would be exposed to aerial attack until it reached another patch of cover. Thus, the most risk-averse immediate behavior would be to remain stationary.

Our experimental site comprised a natural clearing, surrounded predominantly by oak shrubs (*Quercus geminata* and *Q. myrtifolia*). We constructed a brushpile of stacked leafless oak branches in the clearing, 3.5 m from living shrubs. The brushpile was 2 m in diameter and 0.8 m high. A camouflaged cloth blind positioned
7 m from the brushpile allowed us to observe the behavior of the birds.

A 100 × 50 × 25 cm wire-mesh cage was positioned within the edge of the brushpile. We placed each bird in the cage, then returned to the blind and allowed 1 min for the bird to settle. We then triggered the opening of the spring-loaded cage door. Most (91%) Gray Catbirds released in this manner left the cage in <1 min and entered the adjacent brushpile. When the bird entered the brushpile and perched, we triggered the release of a Cooper’s Hawk (Accipiter cooperii) model, mounted in a gliding position and attached to two small pulleys, that rolled freely in response to gravity along an inclined vinyl-coated cable and passed over the brushpile 1.5 m from the ground at a mean velocity of 5.3 m s⁻¹.

We tested all birds between 0800 and 1600 hours EST, and we tested most (75%) before 1200 hours. Tests of fat and lean birds were similarly distributed over the morning to reduce any bias that might result from time of day. As soon as the hawk model approached within 8 m of the brushpile, we started a stopwatch. Observation then continued until the bird left the brushpile or 600 s passed. Although some birds would have stayed longer (up to 1,611 s in early trials), we ended all trials after a maximum of 600 s. Cutting some trials short in this way allowed us to test a greater number of individuals. Operationally, we defined the end of a bird’s behavioral freeze as the point when it first hopped or flew to a new perch. This movement provided a readily visible and unambiguous event to signal the end of a behavioral freeze.

We compared the freeze durations of fat and lean Gray Catbirds using the Mann-Whitney U test (Zar 1984). We selected this nonparametric test because data were not normally distributed and because we had truncated the distribution of freeze times by ending trials at 600 s. We used a one-tailed test because we predicted that fat birds would have greater latency than lean birds to begin movement following exposure to a simulated predator. We used SIGMASTAT, version 3.0 (SPSS, Chicago, Illinois), to calculate statistical results and considered these statistically significant if \( P \leq 0.05 \).

An assumption of our investigation was that Gray Catbirds reacted to the hawk model as a threat. Treatment affected how long birds froze (Kruskal-Wallis \( H = 7.02, \text{df} = 2, P = 0.03, n = 78 \)) and those exposed to the hawk model remained motionless longer than those exposed to either the hexagon model or no model (Student-Newman-Keuls multiple comparison, \( P < 0.05 \); Fig. 1). Furthermore, no Gray Catbird exposed to either the hexagon model or no model gave a “Ratchet” call, a vocalization randomly to one of three treatments: hawk model, hexagon model, and no model. For the hawk-model treatment, we exposed birds to the model as previously described. For the hexagon-model treatment, we released birds as before but then moved a gray model in the shape of a hexagon along the cable. This model moved at the same velocity as the hawk model and had the same silhouette area when viewed from below. For the final treatment, we simply released birds into the brushpile and moved no model overhead. Each treatment group had equal numbers of fat and lean individuals. We then analyzed the effect of the treatments using the Kruskal-Wallis test (Zar 1984) followed by a Student-Newman-Keuls multiple comparison (Zar 1984).

**Results**

Gray Catbirds appeared to treat the hawk model as a threat. Treatment affected how long birds froze (Kruskal-Wallis \( H = 7.02, \text{df} = 2, P = 0.03, n = 78 \)) and those exposed to the hawk model remained motionless longer than those exposed to either the hexagon model or no model (Student-Newman-Keuls multiple comparison, \( P < 0.05 \); Fig. 1). Furthermore, no Gray Catbird exposed to either the hexagon model or no model gave a “Ratchet” call, a vocalization

![Fig. 1](image-url)

**Fig. 1.** Gray Catbirds remained motionless longer after exposure to a model of a flying hawk than when exposed to a hexagon-shaped model or to no model. Treatments having the same letter to the left were not statistically different at \( \alpha = 0.05 \) (Student-Newman-Keuls multiple comparison). Each plot depicts the median (line inside box), the 25th to 75th percentiles (box), the 76th to 90th percentiles (whiskers), and the 91st to 100th percentiles (dots).
associated with alarm (Cimprich and Moore 1995), whereas 35% of those exposed to the hawk model did so. These results provide evidence that the hawk model was appropriate for eliciting antipredator responses from Gray Catbirds.

The mean mass of the Gray Catbirds in the fat group exceeded the mean mass of those in the lean group by 6.1 g, a difference representing 18% of the mass of the lean group (Fig. 2). The mean wing loading of fat birds exceeded that of the lean birds by 3.4 N m$^{-2}$, a difference representing 18% of the wing loading of the lean group (Fig. 2).

Fat affected the behavior of Gray Catbirds. After exposure to the hawk model, birds in the fat group had longer freeze times than birds in the lean group, though both exhibited much variation ($U = 682, P = 0.04, n = 66$; Fig. 3). We detected no differences in latency to begin movement between fat and lean birds tested with the hexagon model or with no model ($U = 79, P = 0.60, n = 26$ and $U = 174, P = 0.47, n = 26$, respectively).

**Discussion**

These results provide evidence that fat affects the predator-avoidance behavior of Gray Catbirds during migratory stopover. Fat birds were more averse to predation risk than lean birds, as shown by their greater latency to resume movement after exposure to the hawk model. During migration, Gray Catbirds vary greatly in the size of their fat stores, and those of the birds we selected for our experiment were not unusually fat or lean for this species. Most (85%) of the Gray Catbirds tested had fat scores of 0, 1, or 3 and, during the 1997 season, most (76%; $n = 1,658$) of the Gray Catbirds captured at the site received these same three scores. Thus, much potential exists within this species for behavioral variation resulting from variation in fat stores.

It has often been assumed that increasing fat stores increase predation risk (e.g., Lima 1986, McNamara and Houston 1990, Houston et al. 1993, Gosler et al. 1995). However, a direct link between fat and the probability of survival has yet to be demonstrated. Several investigations have shown that maneuverability and the take-off performance of birds decrease as mass increases (e.g., Witter et al. 1994, Kullberg et al. 1996, Veasy et al. 1998, Lind et al. 1999) and, although this suggests that birds with more fat reserves experience greater risk, these birds may compensate behaviorally to mitigate this risk. If birds act with greater caution as they accumulate fat, their rate of mortality attributable to predation may, in fact, not increase. This could explain the observation of Whitfield et al. (1999) that Eurasian Sparrowhawks (A. nisus) did not prey on wintering Common Redshanks (Tringa totanus) differentially in relation to the prey’s

**Fig. 2.** Mass and wing loading of Gray Catbirds in the fat and lean groups. Each plot depicts the mean (line inside box) ± one standard deviation (box) and the range (whiskers). Results are based on 33 fat and 33 lean birds.

**Fig. 3.** Fat Gray Catbirds remained motionless longer than lean individuals following exposure to a model of a flying hawk. Plots depict the median (line inside box), the 25th to 75th percentiles (box), the 76th to 90th percentiles (whiskers), and the 91st to 100th percentiles (dots). These results are based on 33 fat and 33 lean catbirds. The $P$ value is based on the Mann-Whitney $U$-test.
body fat. Our investigation provides evidence of a relationship between fat and predator-avoidance behavior and suggests that fat may have a greater effect on antipredator behavior than on actual probability of predation.

There are two potential explanations for the effect of fat on predator-avoidance behavior of Gray Catbirds. One possibility is that increasing fat stores decrease take-off and flight performance and that this compromises the ability to escape the attacks of aerial predators. Another possibility is that fat has its effect on predator avoidance through its influence on motivation to forage. In this case, fat birds remain inactive longer simply because they have less need to initiate foraging. Because these two explanations are not mutually exclusive, they cannot be seen strictly as alternatives. However, our results suggest that fat has its influence on behavior through its effects on flight performance rather than its effect on motivation to forage. We exposed the birds to three treatments: the hawk model, the hexagon model, and no model. If the only factor determining the duration of inactivity was motivation to feed, fat birds should have remained motionless longer than lean birds in all three treatments. However, we detected no differences between fat and lean groups when we tested them with the hexagon model and no model. That an effect of fat was evident only with a simulated aerial predator supports the idea that it was flight performance rather than motivation to forage that determined behavior.

Further support for the idea that flight performance can affect predator-avoidance behavior comes from the results of Witter et al. (1994). These investigators manipulated the flight performance of European Starlings (*Sturnus vulgaris*) by attaching external weights and found that birds carrying greater additional mass spent less time away from protective cover—behavior consistent with increased caution. The weights would not decrease motivation to forage and might even increase it by elevating daily energy expenditure. However, the weights would affect flight performance in the same way that fat does.

Our results suggest that fat should affect the predator-avoidance behavior of a variety of migrant birds. Gray Catbirds are short- to medium-distance migrants that carry moderate fat loads. Many long-distance migrants carry larger loads, often representing up to 100% of their lean body mass (Lindström and Piersma 1993). Furthermore, the habitat use and escape tactics of Gray Catbirds would tend to minimize the importance of flight abilities and, thus, fat, in determining their ability to elude predators. Gray Catbirds escape by flying down into thick vegetation (Lima 1993) and, because they typically forage among shrubs (Cimprich and Moore 1995), escape would require only short flights. Thus, if the behavior of Gray Catbirds is affected by fat, other migrants that forage in more exposed locations should be affected to an even greater degree. Furthermore, it is likely that fat exerts an even stronger influence on the behavior of species that carry particularly large fat loads or that rely heavily on aerial maneuvers for escape.

If the size of a migrant’s fat reserves can affect how long the bird freezes following a close encounter with a predator, it likely influences other aspects of stopover behavior. For example, the effect of fat on vulnerability to predation could be an important factor in determining how, when, and where migrants forage. These, in turn, could affect fat-deposition rates and stopover length. The predation risk associated with fat might even play a role in shaping the maximum size of migrants’ fat reserves. The interaction between fat and predation risk in controlling stopover behavior remains to be fully explored.

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