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Received 9 December 1996, accepted 4 June 1997.
Associate Editor: R. M. Zink

The Auk 115(1):221–223, 1998

Body Mass, Ambient Temperature, Time of Day, and Vigilance in Tufted Titmice

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Risk of starvation and risk of predation are two major evolutionary forces thought to shape an animal's foraging behavior (Lima 1986, McNamara and Houston 1990). If energetic demands are high, the risk of starvation could be high, and individuals should increase their energy reserves by foraging more intensively. If the risk of predation is high, individuals should become more vigilant to detect predators. However, when vigilant for predators, individuals could be forced to reduce other activities such as foraging (e.g. Caraco 1979, Elgar 1989).

McNamara and Houston (1986) modeled vigilance behavior in diurnal animals as a function of energy reserves and time of day. They predicted that vigilance rate should be low in the morning, a time when animals replenish fat stores lost during the nocturnal fasting period. Vigilance also was predicted to be low late in the day as animals accumulated energy reserves for the following night. In contrast, the reduced demand for energy gain around midday was predicted to allow a heightened vigilance rate. We are aware of no empirical tests of these predictions. In the present study, we examined the relationships among vigilance rate, energy reserves (body mass), and time of day in Tufted Titmice (*Baeolophus bicolor*). We also examined the effects of ambient temperature because vigilance has been shown to be positively correlated with temperature (Pravosudov and Grubb 1995).

Methods.—We studied vigilance in six male Tufted Titmice during the winter of 1994–95. The birds were caught at different locations in central Ohio and observed in isolation for eight days in an outdoor aviary 3 × 8 × 2 m high. During that period, food (unshelled sunflower seeds) and water were provided *ad libitum.* The aviary was open to the sky (except for wire netting) but was walled by translucent fiberglass panels that isolated the birds visually and maintained wind speeds within the aviary at or near zero. One end of the aviary was roofed by a translucent fiberglass panel 30 cm wide that protected a "recording" perch and feeder from rain and snow.

We observed the titmice from an observation chamber attached to one end of the aviary. Observations occurred under prevailing photoperiods, and ambient temperatures were recorded and stored every 30 min in a computer housed in an attached observation chamber (Weather Wizard III and Weatherlink software; Davis Instruments). An electronic balance inside the observation chamber was connected through a one-way glass wall to a perch used by the birds frequently during the day and for roosting at night. Readings from the balance were recorded to the nearest 0.01 g and stored in another computer, also housed in the observation chamber.

To evaluate a bird's vigilance, we divided each day into four 2-h blocks from 0900 to 1700 EST. During each block, we randomly selected one 30-min period during which we observed vigilance. We obtained a

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measure of vigilance by recording the number of times a bird "looked up" while perched on a horizontal branch handling and eating a sunflower seed held between its feet. We considered a bird to be looking up when its bill was pointed above the horizontal (Pravosudov and Grubb 1995). Although birds sometimes may have looked up while swallowing food pecked from a seed, they also looked up periodically while removing the shell to obtain access to the seed. Thus, we assumed that looking up during opening and eating of a sunflower seed represented interruption in food intake related to being vigilant. For parids such as the Tufted Titmouse, measuring vigilance while the bird is handling a food item seems to be more valid than while a bird is foraging, during which it also could be looking up to scan for prey items or for another foraging site.

For every observation period, we calculated a mean rate of vigilance (look-ups per s) based on 4 to 30 observations. Thus, we obtained four measures of vigilance per day (one in each time block) for eight days for each bird. Also for each time block, we obtained mean body mass and average ambient temperature.

Statistical analysis.—To test for the effects of body mass, ambient temperature, and time of day on vigilance, we used a repeated-measures ANCOVA with time of day (four levels) as a factor and body mass and temperature as covariates. To investigate whether there was a directional change in vigilance during the day, we also used a nonparametric repeated-measures, ordered alternatives Friedman test for the effect of time of day on vigilance (Hollander and Wolfe 1973). For this analysis, all vigilance records for each bird were reduced to one per time block per day.

Results.—There were significant, positive relationships between titmouse vigilance and both ambient temperature ($b = 0.002$, $t = 2.17$, $P = 0.03$) and body mass ($b = 0.07$, $t = 5.61$, $P < 0.001$). After controlling for these covariates, we also found a significant association between vigilance rate and time of day ($F = 3.23$, df = 3 and 15, $P = 0.05$), with titmice steadily increasing their vigilance throughout the day (Friedman test, $L = 179$, $n = 6$, $k = 4$, $P < 0.001$; Fig. 1). None of the first-order interactions among the two covariates and the factor was statistically significant. Another repeated-measures ANCOVA, with the bird as a random factor and ambient temperature, body mass, and time of day as covariates, produced similar results. Each of the three covariates was positively and significantly related to vigilance (multiple $R^2 = 0.67$, $F = 47.02$, df = 3 and 176, $P < 0.001$; temperature, $b = 0.002$, $t = 2.09$, $P = 0.03$; body mass, $b = 0.07$, $t = 5.52$, $P < 0.001$; time of day, $b = 0.02$, $t = 3.60$, $P < 0.001$). None of the first-order interactions was statistically significant. All of these analyses suggested that the three variables affected vigilance rates independently in Tufted Titmice.

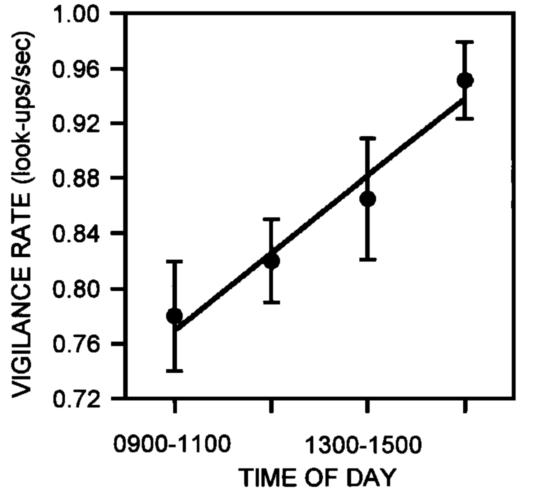

FIG. 1. Relationship between vigilance rate and time of day in six Tufted Titmice. Values are mean ± 1 SE.

Discussion.—That titmice were more vigilant in warmer weather is not surprising. A positive relationship between vigilance rate and ambient temperature has been demonstrated previously for free-ranging Tufted Titmice (Pravosudov and Grubb 1995), Willow Tits (*Parus montanus*; Hogstad 1988), and Yellow-eyed Juncos (*Junco phaeonotus*; Caraco 1979). In lower ambient temperatures, a bird must increase its metabolic rate to maintain body temperature. The higher metabolic rate demands more energy, which requires more intensive foraging. In order to increase its foraging activity at lower ambient temperatures, a bird may compensate by decreasing its vigilance rate. Caraco (1979) and Hogstad (1988) demonstrated the effect of temperature on vigilance rate indirectly through a change in group size which, in turn, was related to ambient temperature. By contrast, Pravosudov and Grubb (1995, this study) found evidence for a direct influence of ambient temperature on vigilance rate, independent of group size.

There was a positive relationship between body mass and vigilance rate within the birds. This finding supports the prediction of McNamara and Houston (1986). Contrary to McNamara and Houston (1986), however, our titmice increased their vigilance rate throughout the day independent of ambient temperature and body mass. We can think of two possible explanations for this result. The first is based on the assumption that a bird with considerable energy reserves, regardless of possible mass-dependent predation risk, can afford more time to be vigilant for predators. The second follows from the assumption that a heavier bird is more easily caught by a predator.

Vigilance rate was positively correlated with body mass independent of time of day. Therefore, when a bird had relatively large fat reserves in the morning, it was more vigilant than when morning reserves were relatively low. We also found that all of the titmice increased their body mass (fat reserves) steadily throughout the day, so that the birds always were lightest in the morning and heaviest in the evening (Pravosudov and Grubb 1997). Therefore, it is possible that vigilance rates were in response to a bird's average level of energy reserves rather than to time of day. McNamara and Houston (1986) argued that animals should be less vigilant in late afternoon because, as evening approaches, time devoted to accumulating energy reserves for the night becomes of paramount importance. However, a safe level of energy reserves for the night already may be achieved sometime nearer midday, particularly in an experiment like ours where birds have access to food *ad libitum.*

The other explanation for the positive relationship between vigilance and time of day derives from the assumption that heavier birds are more vulnerable to predation (e.g. Lima 1986, McNamara and Houston 1990). It has been assumed that heavier birds have higher predation risk because they are less maneuverable and fly more slowly than lighter birds (Witter et al. 1994, Metcalfe and Ure 1995). A heavier bird under higher predation risk may employ a higher vigilance rate to reduce such risk. Because our titmice always were lightest in the morning and heaviest in the evening, it is possible that during the late afternoon heavier birds were more vigilant to compensate for their higher perceived predation risk at that time. We have described these two explanations

partially funded by an Ohio State University Graduate Alumni Research Award and an O.S.U. Presidential Fellowship to V.V.P., and by National Science Foundation Grant IBN-9522064 to T.C.G. The work was carried out under Ohio State University animal use protocol 94A144.

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