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## VIGILANCE IN THE TUFTED TITMOUSE VARIES INDEPENDENTLY WITH AIR TEMPERATURE AND CONSPECIFIC GROUP SIZE<sup>1</sup>

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*Key words:* Vigilance; group size; air temperature; Tufted Titmouse; *Parus bicolor*.

Vigilance in free-living animals has been studied intensively both theoretically and empirically (see Elgar 1989, Lima 1989, McNamara and Houston 1992). When vigilant for predators, an individual must reduce other activities, such as foraging. Therefore, extent of vigilance has been considered the result of a compromise between gathering sufficient food and avoiding predators (Lendrem 1983, 1984; Kaitala et al. 1989). When presented with a choice, birds prefer to forage

near protective cover (Grubb and Greenwald 1982, Lima 1987). Also, as vigilance can provide benefits simultaneously to several individuals foraging together, many studies have concentrated on the relationship between vigilance and group size of conspecific or heterospecific groups (Caraco 1979a, Elgar 1989, Lindstrom 1989, Cimprich and Grubb 1994). Theoretical models of vigilance as a function of group size consider evolutionarily stable levels of vigilance to be affected by such environmental parameters as rates of foraging and predator attacks, and by the internal state of a forager (McNamara and Houston 1992). Although food intake rate and degree of hunger have been considered important determinants of vigilance, the effects of weather conditions, which have been shown to affect birds' foraging behavior (Grubb 1975, 1978; Mayer et

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al. 1979), have rarely been reported in relation to vigilance (Caraco 1979b, Lima 1988, Elgar 1989). Here, we investigate the effects of air temperature, wind speed, solar radiation, seasonal conditions (year), and both conspecific and heterospecific group size on vigilance in Tufted Titmice (*Parus bicolor*) wintering in deciduous woods.

## STUDY AREA AND METHODS

We studied winter foraging ecology of Tufted Titmice in two 20-ha deciduous woodlots in Morrow County, Ohio during the winters of 1992–1993 and 1993–1994. American beech (*Fagus grandifolia*), sugar maple (*A. saccharum*), ashes (*Fraxinus* spp.), and oaks (*Quercus* spp.) were dominant tree species. In November, birds were captured at feeders and color-banded after which the feeders were removed. We observed vigilance in foraging titmice from late December to mid-February. Each bird encountered was followed until it found and handled a large food item (e.g., beechnut, acorn or cocoon). To obtain a measure of vigilance, we recorded the number of times the bird looked up while handling and eating such an item over the course of several minutes. We considered the bird to be vigilant when its bill was parallel with or pointed above the horizontal plane. Such vigilance was easily recognized because titmice keep their head down when hammering at large food items. Indexing vigilance by counting “look-ups” during normal foraging is problematical because Tufted Titmice quite often perch obliquely or even upside down. We noted the total time each food item was handled and the number of look-ups that occurred during that time. For analysis, we used the number of look-ups per second. All observations were made between 09:00 and 14:00.

During each period of observations, we measured air temperature (using a mercury thermometer), wind speed (using an anemometer, “Velometer Jr,” Alnor Instrument Co., Niles, Illinois), and solar radiation (using a heliometer, “Solar Meter,” Dodge Products, Houston, Texas) at several fixed locations and used the daily average values of these weather variables in the analysis. During the period of observations the average daily air temperature varied from  $-23$  to  $+14^{\circ}\text{C}$ , wind speed from 0.3 to 2.48 m/sec, and solar radiation from 2.5 to 46.2 mW/cm<sup>2</sup>.

Birds were considered to be foraging in a group if they followed one another as they moved through a woodlot. For each observation of vigilance (during one bout of food handling), we recorded the number of conspecifics (range 0–3) and heterospecifics (mainly Carolina Chickadees, *Parus carolinensis*, White-breasted Nuthatches, *Sitta carolinensis*, and Downy Woodpeckers, *Picoides pubescens*, range 0–5) present in a group.

For statistical analyses, we used the number of look-ups per second as the dependent variable, and woodlot, seasonal conditions (year), daily average air temperature, wind speed, solar radiation, and the number of conspecifics and heterospecifics in the vigilant bird's group as independent variables. For multiple regression analysis, only one value was used per color-marked individual. That is, the bird was taken as the primary sampling unit. After first testing a model that included

all independent variables and all possible interactions among variables we excluded non-significant variables and interactions successively from the largest  $P$ -value down, and computed the regression again until only significant independent variables and/or interactions remained. We also tested all possible combinations of factors to make sure that the combination with largest  $P$ -values produced the best model (highest  $R^2$ ).

## RESULTS AND DISCUSSION

Thirty-four individual birds were used for the analysis. Only temperature and number of conspecifics in the foraging group were significantly related to vigilance rate. Titmice decreased their vigilance with decreasing air temperature ( $b_1 = 0.008$ ,  $t = 3.06$ ,  $P = 0.005$ , Fig. 1) and with increasing number of conspecifics ( $b_2 = -0.062$ ,  $t = -2.33$ ,  $P = 0.027$ , Fig. 1). Neither the number of heterospecifics nor the combined total of conspecifics and heterospecifics in a group had a significant effect on titmouse vigilance ( $P > 0.2$ ).

The positive correlation between vigilance and air temperature appears to have a ready explanation. With decreasing temperature, a bird below its lower critical temperature must increase its metabolic rate to maintain its body temperature. The higher metabolic rate demands more energy, which requires more intensive foraging. Thus, our finding supports the hypothesis that vigilance is a trade-off between foraging and predation risk (McNamara and Houston 1992). When a bird has to increase its food-intake rate in lower air temperatures, it compensates by decreasing its vigilance time. Caraco (1979b) found that group size in Yellow-eyed Juncos (*Junco phaeonotus*) was negatively related to air temperature and that vigilance of these birds was negatively related to their group size. The same results were obtained for Willow Tits (*Parus montanus*) in Norway (Hogstad 1988). Thus, air temperature seems to cause variation in vigilance not directly, but through a change in group size although this is not certain since the group size and air temperature covaried. In our study, group size was not affected by air temperature ( $P > 0.3$ ) which gives us more direct evidence of the effect of temperature on vigilance independent of group size.

Although group size has often been shown to affect vigilance (e.g., Studd et al. 1983, Caraco 1979b, Elgar 1989), such an effect can be complex in multispecies foraging groups. Our study showed that only the number of conspecifics was significantly related to titmouse vigilance. Titmice were less vigilant when in the company of more conspecifics, but their vigilance was not responsive to the number of individuals of other bird species in the group. That the number of heterospecifics in a group did not affect titmouse vigilance suggests that the foraging efficiency of titmice did not benefit from the presence of the other species. By contrast, some heterospecifics may have actively joined titmice to benefit from titmouse vigilance. This hypothesis has been supported for the Downy Woodpecker, one of the species that join foraging groups of Tufted Titmice. Downy Woodpeckers decreased their vigilance while foraging with parids (Sullivan 1984). It seems that vigilance in large multispecies foraging groups might reflect complex social relationships among these species

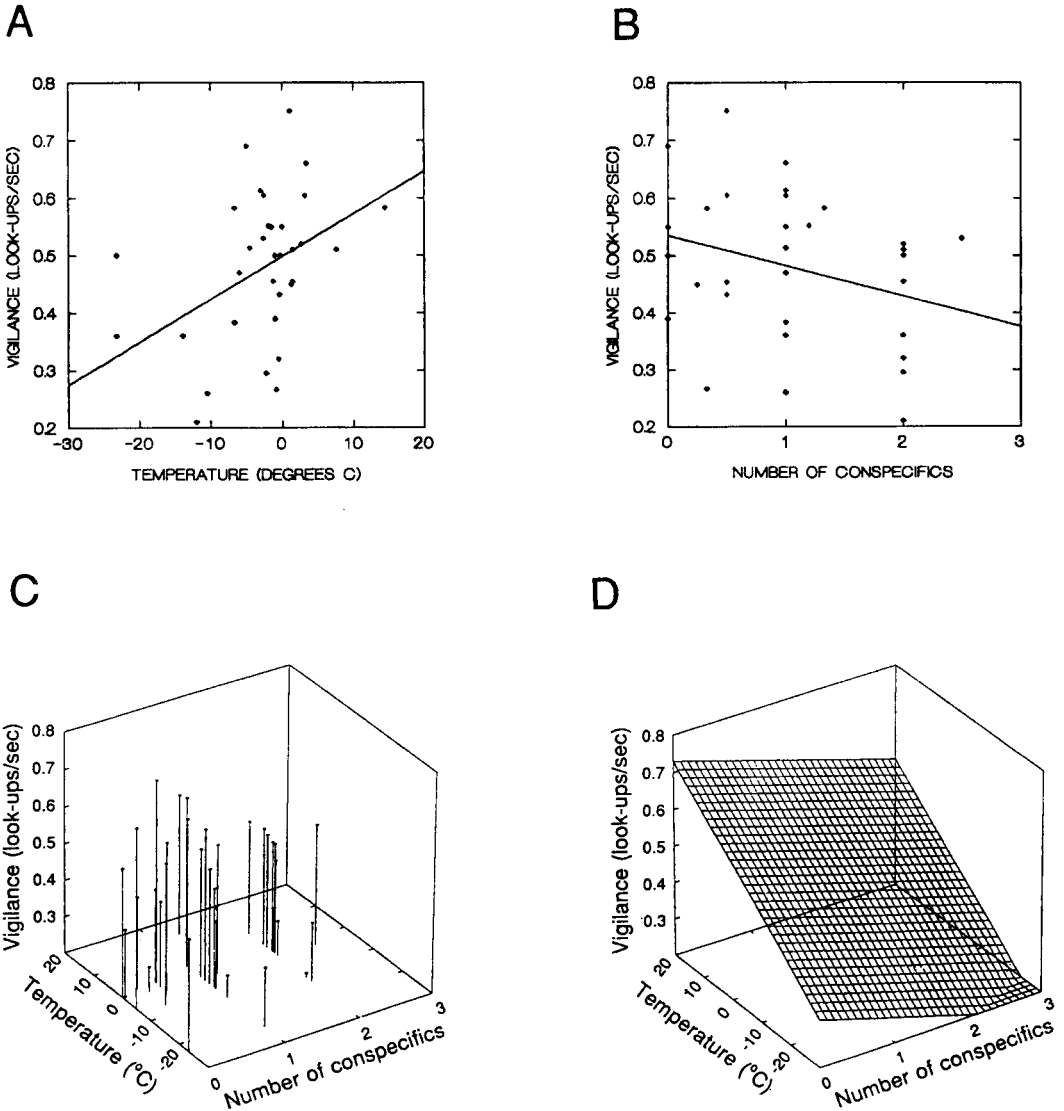


FIGURE 1. Vigilance of wintering Tufted Titmice in relation to (A) air temperature, (B) number of conspecifics, and (C) both temperature and number of conspecifics. The two-factor response plane (D) is based on the equation: look-ups/sec = 0.572 + 0.00825·°C - 0.0619·number of conspecifics.

and might vary in different circumstances. Many bird species decrease their vigilance when accompanied by heterospecific group members (Powell 1974, Popp 1988). Popp (1988) showed that although all three species he studied decreased their vigilance when foraging with the other species, the lowest vigilance was recorded when in the company of conspecifics. Several shorebird species shared their vigilance with other species selectively: their vigilance was not shared with larger species and with species rarely found in the area studied (Metcalf 1984). More studies on vigilance of other bird species foraging with Tufted Titmice are

needed to understand the complex of adaptive responses within such multispecies foraging groups.

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ARTIFICIAL SNAGS AS NESTING SITES FOR CHICKADEES<sup>1</sup>

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Chickadees and titmice are abundant permanent residents that nest in tree cavities. These attributes have made them attractive subjects for study in the heavily managed woodlands of western Europe, where natural cavity sites are rare. Under such circumstances, parids nest readily in nest boxes, fostering a continual stream of experimental projects and long-term demographic studies (e.g., Perrins 1979, Perrins and McCleery 1989, Dhondt 1989, Hogstad 1989).

Compared with those of western Europe, the woodlands of North America are vast and not intensively managed. Cavities and potential cavity sites are usually abundant and, with a few exceptions in coniferous forests of the West (e.g., Dahlsten and Copper 1979, McCallum 1990), attempts to establish nest-box study systems for parids have failed, presumably because the birds' preferences for certain attributes of cavities are better met by natural sites. Therefore, whereas European parids are perhaps the best-studied group of wild, non-game birds in the world, much less is known about their North American congeners (e.g., Grubb and Pravosudov 1994). Here, we introduce an artificial nesting structure (hereafter referred to as a "snag") that appears

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