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LEVELS OF VIGILANCE TRACK CHANGES IN FLOCK SIZE IN THE GREATER FLAMINGO (*PHOENICOPTERUS RUBER RUBER*)

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Los niveles de vigilancia reflejan cambios en el tamaño de las bandadas de Flamencos comunes (*Phoenicopterus ruber ruber*).

Key words: Greater Flamingo, *Phoenicopterus ruber*, nocturnal foraging, diurnal foraging, flock size, Venezuela, vigilance.

INTRODUCTION

Numerous empirical studies in birds have demonstrated a decrease in the proportion of time allocated to vigilance as flock size increases (reviewed by Elgar 1989, Roberts 1996, Treves 2000). The negative correlation between vigilance and group size is usually ascribed to a perceived reduction in predation risk in larger groups and/or to an increase in the intensity of feeding competition (Beauchamp 2003). Because investigations of the group-size effect are often correlational, inferences cannot be made about the causal link between changes in flock size and vigilance. In such cases, several extraneous factors may explain why vigilance decreases in large flocks. The most obvious factor is food density. If large flocks aggregate over areas of high food density, vigilance may be expected to decrease as more time can be allocated to feeding thus making the inverse relationship between flock size and vigilance causally spurious (Elgar 1989).

One possible way to establish a stronger causal link between vigilance and flock size might be to match changes in vigilance with concurrent changes in flock size in the field during a continuous time sequence. Adjustments in vigilance due to the arrival or departure of companions is more likely to be caused by changes in flock size than by changes in extraneous factors, such as food density, since birds are foraging at the same location at nearly the same time. Among the few studies that have used such a matched design, vigilance has been shown to increase after the departure of companions and to decrease after the arrival of companions in foraging Downy Woodpeckers (*Picoides pubescens*) (Sullivan 1984) and in preening Crested Terns (*Sterna bergii*) (Roberts 1995).

Here, we examine changes in vigilance

subsequent to the arrival or departure of companions in flocks of Greater Flamingos (*Phoenicopterus ruber ruber*) foraging in a tropical lagoon complex in Venezuela. Previous correlational work has already documented a reduction in vigilance with variation in flock size in Greater Flamingos (Schmitz & Baldassarre 1992, Beauchamp & McNeil 2003) but it is not clear (i) to what extent variation in vigilance is strongly related to changes in flock size in this species and (ii) what the significance of such a relationship might be. We used the matched design to explore more fully the causal aspects of earlier correlational observations.

METHODS

Study area. We conducted the study at the Chacopata lagoon complex (10°40'N, 63°46'W) on the north side of the Araya Peninsula, Sucre State, northeastern Venezuela, from 20 December 2000 to 6 January 2001. One of us (GB) observed birds near the shore of two lagoons where foraging Greater Flamingos roosted and foraged in large numbers in the non-breeding season. We used 9X35 binoculars for daytime observations (between 15:30 and 17:30 daily) and a binocular light intensification module (ITT Night Quest 250, Monovision Night Vision, Laguna Beach, California) affixed with a 12X camera lens and an infra-red light beam for nighttime observations (between 18:45 and 21:00 daily). Observations were dictated into a portable cassette recorder.

Sampling and statistical analyses. Feeding flocks of Greater Flamingos consisted of birds actively involved in feeding activities and located at least 30 m away from any other flock. We followed at most three different flocks at a single site at each observation period. Observations focused on a single individual in each flock. Since the population was not marked, it is possible that the same individuals may have been sampled more than once but this appears unlikely given the large number of birds in the area at the time (> 200). For each focal bird, sampling of behavior took place over at most 10 min or until the flock changed in size or was lost from sight. The number of birds departing or arriving was noted and the behavior of the same bird, if possible, was sampled one more time after the change in flock size once foraging activities resumed. Occasionally, the focal bird got lost in the shuffle as new birds arrived or left. In those cases, we selected a focal bird close to the area where the previous focal bird had foraged earlier. During each focal observation, we noted whether the focal bird foraged with the head underwater or scanned the surroundings with the head up. The timing of occurrence of all changes in behavior was obtained later from the taped observations.

We calculated the time budget before and after the change in flock size. For each focal observation, mean scan duration refers to the average duration of all sequences with the head up, while mean feeding duration refers to the average duration of all sequences with the head underwater which preceded a sequence with the head up. The overall proportion of time spent with the head up is referred to as vigilance. We used linear regression models to relate changes in mean scan duration, mean feeding duration, and vigilance to changes in flock size.

We also calculated the time budget of focal birds in focal observations that lasted at least 6 min and during which flock size remained the same. The time budget during the first and during the last 3 min of observation was compiled. We used the Wilcoxon signed–ranks test to examine differences in mean scan duration, mean feeding duration, and vigilance within these flocks. Median values along with the interquartile range are presented.

RESULTS

At the two lagoons, Greater Flamingos usually foraged in straight lines within 2 m of each other and moved forward with a scything action of the head. In most cases, individuals joined or left focal flocks by walking. We recorded behavior in flocks that experienced either a decrease (n = 4) or an increase (n = 15) in size. Median flock size before changes in membership was 4 (2.5–10). Behavior was also sampled in 32 flocks that failed to change in size during the observation period. Median flock size in these stable flocks was 16.5 (6.75–25.75).

Mean scan duration decreased after an increase in flock size and increased after individuals left the flock ($F_{1,17}$ = 5.4, P = 0.03; Fig. 1A). After the arrival of new flock members, mean feeding duration increased but decreased when flock size became smaller ($F_{1,17}$ = 6.3, P = 0.02; Fig. 1B). Overall, vigilance decreased when flock size increased and increased when flock size decreased ($F_{1,17}$ = 7.3, P = 0.02; Fig. 1C).

In sequences where flock size remained stable, we failed to document significant changes between the first and last 3 min of observations in mean scan duration [first: 4.8 s (3.3–7.8 s); last: 4.5 s (3.8–6.1 s); P = 0.99], in mean feeding duration [first: 20.3 s (13.6–37.5 s); last: 16.9 s (13.1–29.8 s); P = 0.08] and in vigilance [first: 17% (7–29%); last: 21% (15–25%); P = 0.24].

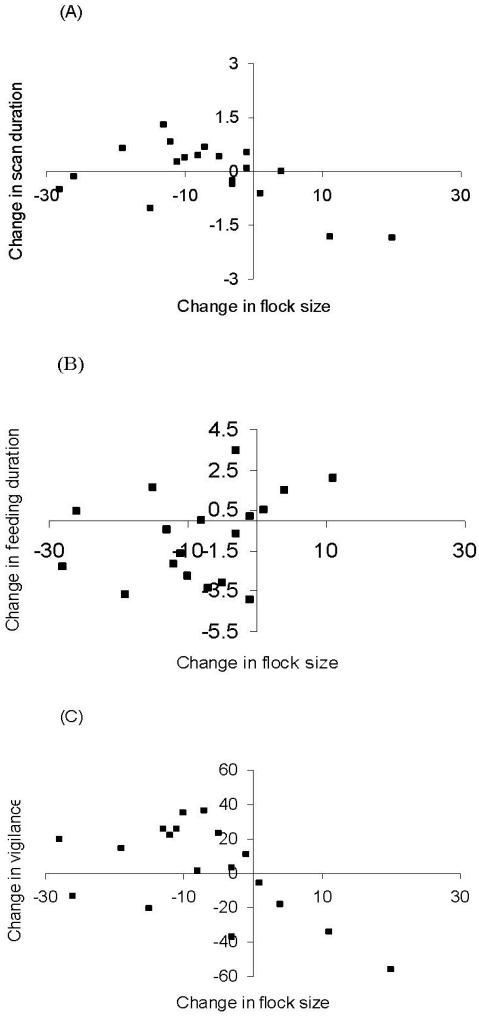

FIG. 1. Changes in mean scan duration (A), mean feeding duration (B) and vigilance (C) as a function of changes in flock size in foraging Greater Flamingos (n = 19). Positive changes in flock size indicate that the focal flock experienced a decrease in size. Similarly, positive changes in mean scan duration, mean feeding duration or vigilance also indicate a decrease as flock size changed during the observation period.

DISCUSSION

Levels of vigilance observed during timed behavior sequences clearly tracked changes in flock size in foraging Greater Flamingos. As flock size increased, birds foraged for longer bouts and reduced scan duration. Vigilance decreased in these newly enlarged flocks. In contrast, birds foraged to a lesser extent as flock size decreased and scanned for longer periods. Vigilance thus increased in these newly reduced flocks. The results are consistent with the findings of several earlier studies

that correlated changes in vigilance with flock size (Elgar 1989, Roberts 1996, Treves 2000). Here, we demonstrate a strong link between changes in flock size and vigilance in a wild foraging bird species. In addition, we show that vigilance in the Greater Flamingo is a dynamic process whereby birds adjust their level of vigilance in response to arrivals to, and departures from, the flock (Broom & Ruxton 1998).

One potential confounding factor in the matched design used in this study is the passage of time which necessarily accompanies any changes in flock size. As time goes by, individuals in a flock may become less wary since sufficient time may have elapsed to assess potential risk factors (Carbone et al. 2003) such as disturbance by people (Yosef 2000). In this case, vigilance may be expected to decrease with time thus masking any reduction due to a subsequent increase in flock size. Similarly, food density may decrease with time or birds may become less hungry. In this case, vigilance may be expected to increase with time thus confounding any increase due to a subsequent decrease in flock size. However, there was no indication that our measures of vigilance varied at the time scale used in the study. The earlier study with Downy Woodpeckers in a foraging context did not control for the potential effects of wariness, food density, or satiation (Sullivan 1984).

Greater Flamingos reacted to the number of birds added to or subtracted from the flock as indicated by significant slopes in the regression models. It remains to be seen over which range of flock sizes Greater Flamingos will still respond to changes in flock size. In addition, it would be interesting to examine whether flocks of different sizes react differently to arrivals and departures. One would assume that changes in behavior may be more pronounced in small flocks which maintain a high level of vigilance and where the scope for adjustments in vigilance is highest. In preening Crested Terns, however, the magnitude of change in vigilance was not related to flock size (Roberts 1995).

The matched design provides a powerful means to examine the effect of flock size on behavior when the effect of extraneous factors, such as food density, is not expected to vary to a large extent over the duration of observations. Once a strong link is established, it becomes possible to examine more clearly how ecological factors, such as predation risk and feeding competition, will influence the relationship between vigilance and flock size. We did not investigate these ecological factors but suggest that this should be the next step in further studies of vigilance behavior.

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