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VARIABILITY IN PARROT FLOCK SIZE: POSSIBLE FUNCTIONS OF COMMUNAL ROOSTS[1]

C. A. CHAPMAN, L. J. CHAPMAN AND L. LEFEBVRE
Department of Biology, McGill University, 1205, av Dr. Penfield, Montreal, Quebec, Canada H3A 1B1

Abstract. This study documents flock size in mixed-species parrot/parakeet flocks in tropical dry forest of Costa Rica. Variability in flock size was quantified on a diurnal basis, between nesting and nonnesting periods, and during departures from roost sites in the early morning. Flock size was greater when animals were congregating near the roost site near dusk than during the rest of the day or when the birds were departing the roost. Flocks were smallest in the first half of the dry season when they are reported to nest. Three hypotheses (Information Center [IC], Diurnal Activity Center [DAC], and a general foraging hypothesis) all make predictions relating the size of specific types of flocks to the density and distribution of food resources. As predicted, by the foraging hypothesis, diurnal flock size was positively related to the density of potential fruit resources, and flocks were largest when resources were uniformly distributed. However, contrary to predictions of the IC and DAC hypotheses, roosting flock size was not related to the density and distribution of food resources. The size of flocks departing roost sites in the morning was small, and evidence suggested that these flocks may have been avoiding following the flocks that left previously.

Key words: *Communal roosts; parrots; group living.*

INTRODUCTION

The ecological literature contains a number of field and experimental studies which have considered determinants of animal group size (Altmann 1974, Pulliam and Caraco 1984). Theoretical and empirical evidence suggests that the density and distribution of resources may constrain the size of animal groups by influencing the number of animals that can efficiently forage together (Bradbury and Vehrencamp 1976, Leighton 1986, Stacey 1986). With respect to roosting flocks of birds, there are two major hypotheses that make predictions concerning flock size and the density and distribution of resources. The Information Center (IC) hypothesis (Ward and Zahavi 1973) suggests that birds congregate in large communal roosts at night to facilitate the exchange of information between members regarding the location of feeding sites. Ward and Zahavi (1973) suggest that the number of birds attending the roost should be largest when the information concerning the location of feeding sites is most valuable. This may occur when food resources are at a low density and are clumped. Caccamise and Morrison (1986) present an alternative view of communal roosting based on movements of individually marked European Starlings (*Sturnus vulgaris*). These authors suggest that individuals only leave their own foraging area to come to communal roosts, and the associated feeding areas, when doing so more than compensates for the cost of travelling to the roost. They suggest that this occurs when there are clumped resources near the roost (see also Caccamise et al. 1983, Fischl and Caccamise 1985, Morrison and Caccamise 1985). With respect to the relationship between roost size and resource distribution, one of the predictions that this hypothesis shares with the IC hypothesis is that as food resources become more clumped, the size of communal roosts should increase. This prediction can be contrasted to the one made by the general foraging literature which suggests that when depletable food resources are rare and clumped, daytime foraging flocks will be small (Bradbury and Vehrencamp 1976). If a group's foraging activity results in the depletion of the resources in the patches they use, the foraging literature suggests that an increase in group size will increase the area to be searched. With an increase in the time spent travelling some point will be reached at which the energy spent in travel exceeds the energy obtained from the environment, and a smaller group size will be advantageous.

The objective of this study is first to document the variability in the size of neotropical mixed-species flocks of parrots and parakeets, and sec-

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ondly to consider predictions relating the density and distribution of food resources to variation in flock size. Parrots are a suitable taxonomic group to examine these predictions since they are highly gregarious animals and feed primarily on the seeds and fruit pulp of a small number of tropical fruiting trees (Janzen 1984). Fruit trees tend to represent isolated patches (Chapman 1988), and it is relatively easy to determine their location and distribution. During a 10-month field study in Costa Rica, we quantified the variability in parrot flock size on a diurnal and seasonal (nesting vs. nonnesting) basis and documented the size, timing, and direction of flocks departing a major roosting site in the morning.

METHODS

STUDY SITE

Field observations were conducted from May 1987 to March 1988 in Santa Rosa National Park, Costa Rica. The area in which the study was conducted was originally tropical dry forest. Over the past 300 years, large areas of the upper plateau were cleared for pasture, but with the establishment of the Santa Rosa sector as a national park in 1971, some areas have gradually reverted to woody vegetation. The vegetation in the Santa Rosa Sector area consists of a mosaic of grassland (*Hyparrhenia rufa*), dry successional semideciduous forest dominated by *Leuhea speciosa, Bursera simaruba, Cecropia peltata, Spondias mombin,* and *Guazuma ulmifolia,* and nearly-pristine semievergreen forest with trees such as *Manilkara chicle, Hymenaea courbaril,* and *Mastichodendron capiri* (Janzen 1986).

The climate of the region is characterized by two distinct seasons; a wet season from late May to December and a dry season encompassing the remainder of the year. The annual rainfall in the Santa Rosa sector averages 1,527 mm. Little if any rain falls in the dry season and the majority of the trees in the dry successional semideciduous forest lose their leaves.

FLOCK COUNTS

Whenever a parrot/parakeet flock was encountered, the following information was recorded: date, time of day, flock size, activity (if feeding, the food item being consumed), and location. When possible, the species composition of the flock was determined. Because of their coloration, the parrots were extremely difficult to see in trees with leaves. Thus, counts were only recorded for flying flocks, flocks that were flushed from trees, or flocks in trees with little or no foliage. To ensure that counts were as independent as possible, counts of flocks seen in the same area as a flock just counted, but which had been lost from sight, were not considered.

One of the major communal roosts of the parrots was near the administration area of the park. This roost was particularly amenable for observations, as there was a small cleared hill directly overlooking the roost site. Near dusk and dawn, flocks near the roost were very active and vocal. The size of flocks arriving at roost sites tended to be large, and often the number of animals that they contained had to be estimated. For analytical purposes we classified flocks into three different categories; departing flocks, roosting flocks, and daytime foraging flocks. Departing flocks were those flocks seen early in the morning (prior to 06:30) that appeared to be leaving the area of the roost site. Roosting flocks were meant to represent the number of animals attending the communal roost. The size of roosting flocks was difficult to determine since they contained many individuals that approached the area from a number of different angles as daylight was fading. However, estimating their size was facilitated by characteristic behaviors of the parrots near the roost. Just prior to dusk, the parrots would often fly as a single flock, circling the area before settling into the roost tree. The number of birds attending the roost on a particular night was considered to be the largest estimated number of birds seen circling the roost site. Although this may be an underestimate, we believe this is a suitable method for estimating relative change in the size of the roosting flock. Daytime foraging flocks were considered as any flock seen away from the roost.

To examine if some birds followed other birds leaving the roost in the morning, two observers were stationed on the hill above the roost on 12 occasions. For each flock of birds leaving the area near the roost, we recorded the time of departure, flock size, the direction of their departure, and if possible, the species composition of the flock. We followed all departing birds until they were out of sight (approximately 700 m). Often departing flocks divided after approximately 300 m. When this occurred the size and direction of each of the new flocks were recorded.

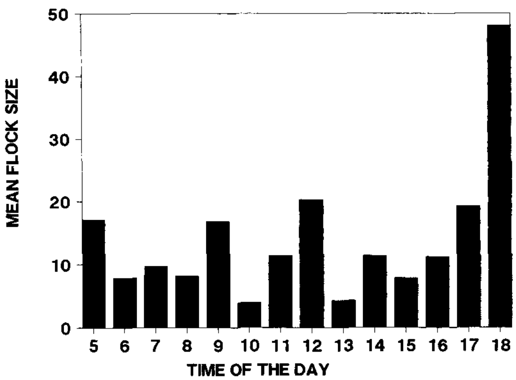

FIGURE 1. The mean size of parrot/parakeet flocks on an hourly basis in Santa Rosa National Park, Costa Rica.

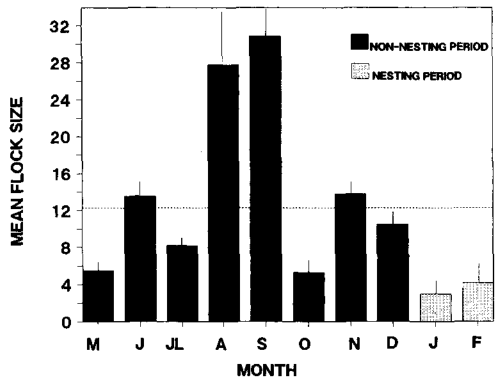

FIGURE 2. The mean size of parrot/parakeet flocks on a monthly basis in Santa Rosa National Park, Costa Rica from May 1987 to February 1988 (flocks seen early in the morning include some flocks leaving the roost, flocks seen late at night include flocks congregating at the roost but not the total roosting flock; the dotted line represents the flock size expected if the distribution of flock sizes between months was uniform).

ECOLOGICAL PARAMETERS

The density and distribution of potential food resources were derived from an ongoing study of 29 fruiting species and the foraging strategies of three species of primates (Chapman and Chapman, unpubl.). A variety of frugivores, including parrots, were observed feeding on many of these tree species over the course of the study. Data were derived from three 4-ha grids divided into 10-m by 10-m cells. The location and size (diameter at breast height, dbh) of all trees of the 29 tree species greater than 5 cm in diameter were recorded. Approximately once every 3 or 4 weeks, tree species were enumerated for the presence of fruit. The spatial distribution of the trees bearing fruit in a particular month was represented by the coefficient of dispersion (CD; Pielou 1969, Sokal and Rohlf 1981). On average, considering the species and sizes examined, there were 33 trees/ha bearing fruit in any given month, but this value ranged from 6.6 to 48.1 trees/ha (Chapman 1988). Since the dbh of tropical fruiting trees has been shown to accurately reflect the fruiting capacity of individual fruiting trees (Peters et al. 1988), we represented potential food abundance as the density of the trees fruiting in a month, weighted by their dbh.

RESULTS

DESCRIPTION OF FLOCK-SIZE VARIABILITY

Over the 10 months of the study, 432 flocks were counted. Flocks contained individuals of four species; White-fronted Parrots (*Amazona albifrons*), Orange-fronted Parakeets (*Aratinga canicularis*), Orange-chinned Parrots (*Brotogeris jugularis*), and Yellow-crowned Amazon parrots (*Amazona ochrocephala*). Over the duration of the study the proportion of the birds identified as being one of the four species did not vary between months for any of the species by more than 6% (n = 89).

The size of the flocks observed at different hours of the day was highly variable (range = 4–48, Fig. 1). The mean size of roosting flocks (55.4 individuals) was much larger than daytime foraging flocks (8.1 individuals) and departing flocks (13.6 individuals). The sizes of all three flock categories were significantly different from each other (Kruskal-Wallis and a posteriori multiple comparisons test $P < 0.05$, Conover 1980). The early morning observations at the roost site similarly suggest that the large roosting flocks rapidly break up into smaller flocks as they leave the roost site.

Flock size exhibited considerable month-to-month variability (range = 3–29, Fig. 2). The observed monthly distribution of flock sizes was tested against a uniform distribution based on the overall mean flock size. The observed distribution differed significantly from uniform ($\chi^2 = 69.8, P < 0.001$, df = 9). January and February were the months with the smallest mean flock sizes. In these months at least one of the species (*Brotogeris jugularis*) is reported to be nesting (Janzen 1984).

TABLE 1. Correlations between food abundance (density of food resources weighted by the size tree), distribution of food resources, and the size of three types of parrot flocks observed in Santa Rosa National Park, Costa Rica.

	Total sample	Mean flock	Nonnesting
		Food abundance	
Departing flock	$r = 0.119, P = 0.336$	13.6	$r = -0.089, P = 0.677$
Daytime foraging	$r = 0.280, P < 0.001$	8.1	$r = 0.195, P = 0.001$
Roosting	$r = -0.04, P = 0.847$	55.4	$r = 0.033, P = 0.800$
		Distribution of food resources	
Departing flock	$r = -0.089, P = 0.472$	13.6	$r = 0.290, P = 0.825$
Daytime foraging	$r = -0.184, P < 0.001$	8.1	$r = -0.082, P = 0.127$
Roosting	$r = 0.078, P = 0.706$	55.4	$r = 0.117, P = 0.603$

ECOLOGICAL DETERMINANTS OF FLOCK SIZE

Ecological theory predicts that when animals are feeding on depleting resources, group size will be largest when resources are abundant and uniformly distributed (Bradbury and Vehrencamp 1976). In contrast, one prediction of both the IC and DAC hypotheses is that roosting flock size will be largest when resources are rare and clumped. To examine these hypotheses we considered the relationships between ecological parameters and flock size for departing, daytime foraging, and roosting flocks separately. The size of daytime flocks was related to both the density and distribution of fruit resources (Table 1). In contrast, neither departing flocks nor roosting flocks were related to these ecological parameters (Table 1). When the months during which parrots have been reported to nest (January and February) were excluded from the analyses, the size of the daytime foraging flocks was not related to the distribution of resources. However, departing and roosting flocks showed a similar nonsignificant pattern and daytime foraging flock size was again positively related to food abundance.

ROOST DEPARTURES

The pattern with which parrots dispersed from the roost site was documented on 12 mornings. The birds tended to restrict their departure routes by not flying large distances over stretches of open grassland. The area near the roost site comprised patches of forest connected by narrow forested strips. The parrots almost exclusively used these strips to travel between forested areas. As a result, there were generally six routes used when departing the roost. We categorized the direction of every flock leaving the general area of the roost (follower) relative to the flock that left immediately prior to it (leader). If flocks were leaving the roost at random, one would expect one in every six leaving flocks to head in the same direction as the preceding flock. We assume that all routes were equally attractive to the birds, as the choice of which of the six directions to take when leaving the roost did not differ from random ($\chi^2 = 5.65$, $P > 0.25$, df $= 5$). Of 41 flocks seen leaving the roost site, only two of the flocks followed the preceding one which differs significantly from random departure ($\chi^2 = 4.1$, $P < 0.05$, df $= 1$). This may suggest that departing flocks avoid each other.

DISCUSSION

It is generally agreed that avian communal roosting behavior is unlikely to provide only one type of benefit (Crook 1965, Weatherhead 1983). The evidence presented here for roosting flocks of parrots does not support one prediction made by both the IC hypothesis and the DAC hypothesis: that roosting flock size should increase as food becomes more clumped. Our data suggest instead that parrots did not congregate at the roost site when information was most valuable or when they could compensate for the cost of travelling to the roost by feeding on clumped resources near the roost. The IC hypothesis also suggests that unsuccessful foragers follow more successful individuals to their feeding sites when they leave the roost (Ward and Zahavi 1973, Krebs 1974, de Groot 1980, Waltz 1987). Although we cannot address the issue of whether the individuals within the flocks that dispersed from a roost were following each other, there was no evidence to suggest that flocks followed each other. In fact, we have presented evidence to suggest that flocks may tend to avoid heading in the direction taken by the preceding flock. The parrots departing roost sites in the early hours of the morning tended to leave in small groups and, it would appear, in a dispersive fashion. If, when leaving a roost, parrots avoid following preceding groups, the probability of arriving at a fruit tree that has conspecific competitors or that has already been depleted may be lower than if departure routes were similar among flocks. Thus, roosts may serve to facilitate dispersion of foragers and minimize intraspecific competition for food resources.

This does not preclude other functions for roosting. Our *Foraging Dispersion Hypothesis* and the IC and DAC hypotheses are clearly not mutually exclusive. Following may occur between individuals in a roost while successive flocks departing a roost avoid the preceding flock's departure route.

The relationship between the size of the diurnal flocks and the density and distribution of food resources suggests that diurnal flock size may have been influenced by foraging efficiency (Altmann 1974, Bradbury and Vehrencamp 1976, Leighton 1986, Stacey 1986). Animals must forage over an area that meets their energetic requirements. If resources are depleted, an increase in group size will increase the area to be searched. With an increase in the time spent travelling, some point will be reached at which energy spent in travel exceeds the energy obtained from the environment, and a smaller group size will be advantageous. Following this logic, and assuming that parrots delete the patches they use, conditions that would increase the need to travel, would decrease group size. The diurnal parrot flocks we observed were smallest when fruit density was low and clumped. This suggests that when parrots have to travel a long distance between feeding sites, they attempt to reduce the distance they must travel by decreasing the number of animals feeding at the site. This may allow animals to stay longer in each patch they visit, as it would take longer for the flock to deplete the tree.

The findings of this study suggest that the size of the parrot flocks may reflect individuals responding to different ecological pressures at different times of the day. In the day, parrots may be adopting a flock size which is suitable to maintain a low level of feeding competition. At night other factors may determine the number of animals attending the roost, but at dawn the roost may function to reduce potential feeding competition by dispersing foragers.

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