

without ripe fruit. The occurrence of a superabundant food source in close proximity to a territory may elicit divergent foraging strategies from the same individual. Plasticity in foraging behavior and social organization was also described in the White Wagtail (*Motacilla alba*) (Zahavi 1971) and the Acorn Woodpecker (*Melanerpes formicivorus*) (Stacey and Bock 1978). The distribution and abundance of food also seem to be the main factors determining the strategies used by these birds.

I thank Meri Cummings and Oscar T. Owre for help with the banding and Steven Green for help with the statistics. I am grateful to Julio E. Cardona for sharing his Mockingbird observations with me and the Tropical Audubon Society for providing research funds. Theodore H. Fleming, Herbert W. Kale, II, Edwin O. Willis, and an anonymous reviewer critically read the manuscript and provided useful comments.

#### LITERATURE CITED

- BEAL, F. E. L., W. L. MCATEE, & E. R. KALMBACH. 1916. Common birds of southeastern United States in relation to agriculture. U.S. Dept. Agr. Bull. 755.
- BEGON, M. 1979. Investigating animal abundance: capture-recapture for biologists. Baltimore, Maryland, University Park Press.
- BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Natl. Mus. Bull. 195.
- CARLETON, A. R., & O. T. OWRE. 1975. The Red-whiskered Bulbul in Florida: 1960–71. *Auk* 92: 40–57.
- HAILMAN, J. P. 1960. Hostile dancing and fall territory of a color-banded Mockingbird. *Condor* 62: 464–468.
- HOWELL, A. H. 1932. Florida bird life. New York, Coward-McCann, Inc.
- KALE, H. W., II, & W. L. JENNINGS. 1966. Movements of immature Mockingbirds between swamp and residential areas of Pinellas County, Florida. *Bird-Banding* 37: 113–120.
- LASKEY, A. R. 1936. Fall and winter behavior of Mockingbirds. *Wilson Bull.* 48: 241–255.
- LONG, R. W., & O. LAKEA. 1971. A flora of tropical Florida. Coral Gables, Florida, Univ. Miami Press.
- MICHENER, H., & J. R. MICHENER. 1935. Mockingbirds, their territories and individualities. *Condor* 37: 97–140.
- MICHENER, J. R. 1951. Territorial behavior and age composition in a population of Mockingbirds at a feeding station. *Condor* 53: 276–283.
- MOORE, F. R. 1977. Flocking behaviour and territorial competitors. *Anim. Behav.* 25: 1063–1065.
- . 1978. Interspecific aggression: toward whom should a Mockingbird be aggressive? *Behav. Ecol. Sociobiol.* 3: 173–176.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill Book Co., Inc.
- STACEY, P. B., & C. E. BOCK. 1978. Social plasticity in the Acorn Woodpecker. *Science* 202: 1298–1300.
- ZAHAVI, A. 1971. The social behaviour of the White Wagtail *Motacilla alba alba* wintering in Israel. *Ibis* 113: 203–211.
- ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice-Hall, Inc.

Received 4 February 1980, accepted 9 June 1980.

#### Avian Time Budgets and Distance to Cover

THOMAS CARACO,<sup>1</sup> STEVEN MARTINDALE, AND H. RONALD PULLIAM<sup>2</sup>

*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA*

One version of the “many eyes hypothesis” proposes that flocking is advantageous, because an individual group member may spend less time scanning for predators and more time feeding than a solitary

<sup>1</sup> Present address: Department of Biology, University of Rochester, Rochester, New York 14627 USA.

<sup>2</sup> Present address: Department of Biology, State University of New York, Albany, New York 12222 USA.

(Pulliam 1973). A number of species allocate time to these behaviors in a manner dependent on flock size, as predicted by the hypothesis (reviewed by Lazarus 1979; Caraco 1979a, Barnard 1980, Bertram 1980). The advantages of group membership may be partially offset, however, when flock members expend time and energy fighting one another (Pulliam 1976, Caraco 1979b).

For several years we have studied winter flocks of the Yellow-eyed Junco (*Junco phaeonotus*). The population is characterized by a linear dominance hierarchy, and dominants defend patches of higher seed density. Dominants may promote their long-term survivorship by aggressively reducing flock size and thereby conserving food for future consumption (Fretwell 1972). The relative advantages of flocking to lower ranking birds, then, may depend on the decrease in scanning time versus the increase in interference time as flock size increases. This comparison depends on several environmental variables, because time budgets vary not only with flock size, but with ambient temperature, seed density, and the proximity of a raptor (Caraco 1979a, Caraco et al. 1980).

Barnard (1980) finds that an individual in a flock of any given size scans for predators more often as the distance to cover increases. When foraging far from cover, individuals are likely to scan for predators more often and reduce fighting, because earlier detection of a predator should be required to maintain an acceptable probability of escaping an attack. If the reduction in aggression far from cover results in increased feeding time, flock size should increase with distance from cover. If increased scanning far from cover results in a decrease in feeding time as well as aggression, however, flock size should be smaller far from cover. To examine these possibilities, we manipulated the availability of cover from predators.

We baited a small area (3 m<sup>2</sup>) with millet (*Panicum miliaceum*) and replenished the food every other day. The nearest natural cover was 6 m away. At natural feeding sites the mean distance from the center of a junco flock to cover is 2.9 m. We recorded behavioral data for 5 days (before cover treatment) and then mounted a small fir tree (*Abies* sp.), 1.5 m high, on a stand next to the baited area. The juncos readily flew into the tree when flushed. We recorded behavioral data for 10 days with the tree in place (with cover treatment). Finally, we removed the tree and recorded observations for another 10 days (after cover treatment). Because junco flocking behavior is temperature dependent (Caraco 1979a), we restricted data collection to temperatures of 3–6°C and 12–15°C.

To estimate time budgets, we first noted flock size and then recorded the behavior of randomly selected focal animals (Altmann 1974) at 15-s intervals. Each observation categorized the behavior as feeding (search for and handling of seeds), scanning for predators, or interference (aggressive interaction and quick movement away from nearby birds). The behavioral states are defined to be mutually exclusive and exhaustive. The different categories are distinguished easily in this species.

Flock size was recorded every 30-s. We entered a zero if the site was unoccupied. Whenever the site was unoccupied, we recorded the elapsed time until a junco arrived at the site to forage. These data allowed us to estimate the arrival rate at a flock size of zero birds. The arrival rate at zero should provide a measure of site quality, independent of the attraction or repulsion of any birds feeding at the site (Caraco 1980). We suspected that site quality measured in this way would decrease with lack of cover.

Table 1 summarizes time budgets for the various temperature-cover treatments. Data are provided for flock sizes 1, 3 or 4, and 6 or 7 birds. In general, when cover was available, the juncos spent less time scanning and more time in interference. Comparing With Cover and No Cover (i.e. Before and After Cover) treatments at 3–6°C, we found that the proportion of an individual's time spent scanning was significantly less with cover for solitaries ( $P < 0.005$ , likelihood ratio test) and for flocks of 3 or 4 ( $P < 0.025$ ). Individuals in flocks of 6 or 7 scanned less often with cover present, but the difference was not statistically significant. At 12–15°C, the proportion of time spent scanning when cover was present was significantly less than the estimate without cover for flocks of 3 or 4 ( $P < 0.05$ ) and for flocks of 6 or 7 ( $P < 0.005$ ). Solitaries scanned more often without cover, but the difference was not statistically significant. At both temperatures individuals in multi-member groups spent less time in interference when cover was not available.

When cover was present, the decrease in scanning as flock size increased was approximately the same as the increase in interference time, so that time feeding was independent of flock size. When cover was absent, however, the average feeding time for an individual in a flock was greater than a solitary's feeding time in seven or eight possible comparisons (within both temperature and separate cover treatment, but across flock size). Thus, flocking may confer a net advantage (at least for subordinates) when individuals exploit resources in an area without nearby cover (Fretwell 1972). As distance to cover increases, scanning increases in any given flock size, and interference, constrained by the immediate requirements of predator avoidance and feeding, decreases.

TABLE 1. Time budgets for different temperature-cover treatments.  $T_S$  is the proportion of time spent scanning for predators;  $T_F$  is the proportion of time spent feeding;  $T_I$  is the proportion of time spent in interference.  $n$  is the sample size. The standard error of flock size is given.

Temperature and cover		Flock size			Mean flock size
		1	3-4	6-7	
3-6°C					
Before cover	$T_S$	0.66	0.48	0.34	$\bar{G} = 1.49 \pm 0.21$
	$T_F$	0.34	0.47	0.57	
	$T_I$	0.00	0.05	0.09	
	$n$	61	106	100	
With cover	$T_S$	0.45	0.40	0.31	$\bar{G} = 2.59 \pm 0.31$
	$T_F$	0.55	0.50	0.53	
	$T_I$	0.00	0.10	0.16	
	$n$	132	156	135	
After cover	$T_S$	0.62	0.60	0.46	$\bar{G} = 1.50 \pm 0.31$
	$T_F$	0.38	0.38	0.42	
	$T_I$	0.00	0.02	0.12	
	$n$	62	61	67	
12-15°C					
Before cover	$T_S$	0.59	0.35	0.35	$\bar{G} = 0.92 \pm 0.23$
	$T_F$	0.41	0.52	0.47	
	$T_I$	0.00	0.13	0.18	
	$n$	22	23	17	
With cover	$T_S$	0.55	0.29	0.12	$\bar{G} = 2.21 \pm 0.17$
	$T_F$	0.45	0.52	0.51	
	$T_I$	0.00	0.19	0.37	
	$n$	212	304	140	
After cover	$T_S$	0.70	0.45	0.34	$\bar{G} = 1.34 \pm 0.16$
	$T_F$	0.30	0.47	0.44	
	$T_I$	0.00	0.08	0.22	
	$n$	23	49	136	

Now, we consider whether a bird should forage near cover or far from cover by comparing feeding time with and without cover available. The juncos spent less time in interference when the tree was not present, but this advantage was outweighed by the disadvantage of increased scanning time. Even though interference time was greater with cover available, seven or eight comparisons for multi-member flocks (within temperature and within group size, but across cover treatment) show that feeding time was still greater with nearby cover provided. Presented with a choice between feeding sites near and far from cover, juncos prefer sites close to cover despite the greater level of aggression. This preference is reflected in the arrival rate when group size is zero. With cover available, an average of 0.32 birds/min (95% confidence interval: 0.23-0.41) arrived when no other birds were present, as compared to 0.19 birds/min (0.14-0.25) before the tree was present and 0.21 birds/min (0.14-0.25) after it was removed. Because the site was more often left unattended when cover was not available, the average group size was larger when the tree was present (see Table 1). Therefore, even though aggression was greater with cover available, flocks were larger, because (we believe) feeding time was also greater, and nearby cover provided greater protection from predation.

Distance to cover influences the quality of a foraging site, and juncos' time budgets vary predictably with distance to cover. When juncos are far from cover, scanning increases and aggression decreases. In small flocks, however, the decrease in aggression does not compensate for the increase in scanning, and feeding time decreases far from cover. Distance to cover is, then, another variable affecting junco flock size, and its impact is mediated, at least in part, through variation in time budgets.

We thank T. S. Whittam and W. A. Cornell for assistance. This study was supported by a U.S. National Science Foundation grant (DEB77-0341) to H. R. Pulliam.

#### LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior sampling methods. *Behaviour* 49: 227-267.

- BARNARD, C. J. 1980. Flock feeding and time budgets in the house sparrow (*Passer domesticus*). *Anim. Behav.* 28: 295-309.
- BERTRAM, B. C. R. 1980. Vigilance and group sizes in ostriches. *Anim. Behav.* 28: 278-286.
- CARACO, T. 1979a. Time budgeting and group size: a test of theory. *Ecology* 60: 618-627.
- . 1979b. Time budgeting and group size: a theory. *Ecology* 60: 611-617.
- . 1980. Stochastic dynamics of avian foraging flocks. *Amer. Natur.* 115: 262-275.
- , S. MARTINDALE, & H. R. PULLIAM. 1980. Avian flocking in the presence of a predator. *Nature* 285: 400-401.
- FRETWELL, S. D. 1972. Populations in a seasonal environment. *Monogr. Pop. Biol.* 5: 1-219.
- LAZARUS, J. 1979. The early warning function of flocking in birds: an experimental study with captive *Quelea*. *Anim. Behav.* 17: 855-865.
- PULLIAM, H. R. 1973. On the advantages of flocking. *J. Theoret. Biol.* 38: 419-422.
- . 1976. The principle of optimal behavior and the theory of communities. Pp. 311-332 *in* Perspectives in ethology (P. H. Klopfer and P. G. Bateson, Eds.). New York, Plenum Press.

Received 3 March 1980, accepted 12 June 1980.

### Forced Copulation in Captive Mallards I. Fertilization of Eggs

JEFFREY T. BURNS, KIMBERLY M. CHENG, AND FRANK MCKINNEY  
*Department of Ecology and Behavioral Biology, Bell Museum of Natural History,  
University of Minnesota, Minneapolis, Minnesota 55455 USA*

Forced copulation (FC) has been reported in a number of avian families but it is especially well known in waterfowl (family Anatidae). Often this behavior has been called "rape" in the bird literature, but we feel that it is best to avoid this controversial term. In contrast to pair copulations, which are typically preceded by characteristic displays by both sexes, FCs are preceded by active pursuit, grasping, and overpowering of the female. Ever since Heinroth (1910, 1911) drew attention to this phenomenon, there has been controversy about its significance, especially in the Mallard (*Anas platyrhynchos*) and other dabbling ducks (tribe Anatini). Geyr von Schweppenberg (1924) thought that it occurs after females start incubating and are no longer available to satisfy the sexual urges of males. Christoleit (1929a,b) believed that females do not really try to escape but rather encourage males to chase them and to compete for copulations, thereby ensuring fertilization by the strongest male. Weidmann (1956) concluded that FC is associated with territoriality and is a mechanism whereby a male discourages other pairs from settling on his breeding area. Bezzel (1959) and Wüst (1960) doubted that it is common enough in wild birds to be of significance, and they attributed its occurrence in parks and zoos to abnormally high densities of birds.

In a key study of wild Pintails (*A. acuta*), Smith (1968) demonstrated that aerial pursuits (including FC attempts) peaked in frequency during the egg-laying period, and he suggested that these copulations could be related to fertilization of eggs. Reports that male urban Mallards make FC attempts on their own mates (Bezzel 1959, Raitasuo 1964) have been confirmed by recent studies, and the occurrence of such imposed pair copulations soon after a female has been subjected to FC strongly suggests that sperm competition is going on [Barrett 1973, Barash 1977 for Mallards; McKinney 1975, McKinney and Stolen in prep., for Green-winged Teal (*A. crecca*)]. The experiment on captive Mallards by Elder and Weller (1954), in which they removed males from their mates and checked the fertility of eggs subsequently laid, had already shown that females can store sperm for up to 10 days. Thus, at least in certain species of