FLOCK SIZE AND THE ORGANIZATION OF BEHAVIORAL SEQUENCES IN JUNCOS

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ABSTRACT.—The sequential organization of scanning for approaching predators and pecking for food was investigated by analyzing films of Yellow-eyed Juncos (*Junco phaeonotus*). The birds were photographed as they fed in small winter flocks in southern Arizona. For a given group size, the probability that a bird scans after each peck was found to be a constant. However, this probability decreased as flock size increased. The organization of sequences of scanning and pecking can be depicted as a simple Markov chain where an environmental variable, group size, probabilistically governs the change from pecking to scanning. In conclusion, flock size influences the frequency distribution of the number of consecutive pecks for food.

The temporal organization of an individual's behavior reflects an interaction of both internal and external factors. For example, a foraging sparrow might consider energy requirements and nutritional constraints (internal variables) along with food density and the rate at which predatory attacks occur (external variables) in deciding how much time to allocate to different activities. In an analysis of shorebird foraging, Baker (1973) suggested that sequences in an individual's behavior can be depicted similarly. He hypothesized that internal, neural mechanisms impart a statistical pattern to the duration of a behavior, but the values of the parameters of the duration process depend on environmental variables. As an example, the number of times a bird steps (hops) between food-searching attempts might always follow a certain type of frequency distribution, but the mean of the distribution is likely to be inversely related to an important external variable, food density.

Suppose a bird performs only two different behaviors (designated by A and B). An observed sequence of an individual's behavior might yield the following: A B A A A B B A A B . . . , or any other sequence of intermingled A's and B's. If one is interested in the temporal aspects of behavior A, it is a simple matter to count the length of each sequence where A occurs until B is initiated. Let L, a random variable, represent the length of sequences of behavior A; the terms length and duration will refer specifically to the number of consecutive occurrences of a given behavior. Then $f(L)$ is the probability function describing the discrete distribution of sequence lengths. In essence, Baker's (1973) hypothesis states that internal mechanisms determine the type of distribution describing $f(L)$, e.g., geometric or logarithmic, but the distribution's parameter(s) should change predictably as important environmental variables change. Therefore, certain attributes of sequence length, such as mean duration, should depend on external factors.

This paper analyzes the sequential pattern of feeding and scanning for predators in Yellow-eyed Juncos (*Junco phaeonotus*). These granivorous sparrows often feed in small flocks during the nonbreeding season. The study was conducted in order to examine the role played by group size, an external variable, in governing the sequential organization of an individual flock member's behavior.

A SIMPLE MODEL

The amount of time an individual spends watching for approaching predators is functionally related to social group size in many birds. Hoogland (1979) and Lazarus (1979) reviewed several examples (also see Barnard 1980 and Bertram 1980). In Yellow-eyed Juncos, the mean rate at which an individual scans for predators is a significantly decreasing, nonlinear function of flock size (Caraco et al. 1980a). Although more time is spent in aggressive interactions as flock size increases, the mean rate at which an individual pecks for food still increases with the size of the foraging group (Caraco 1979). Hence, variation in time budgeting appears to explain some of the advantages of winter flocking in this species (Pulliam 1975, Caraco et al. 1980b), and may be an important aspect of group foraging in Dark-eyed Juncos (*J. hyemalis*; Ketterson 1978). The simple model outlined below attempts to more fully describe these observations by examining sequential patterns in junco behavior.

First, I assume that flocks of all sizes exploit areas with the same seed density, so that food availability is eliminated as an external variable. Also, I assume that the rate at which predators attack is independent of flock size (a realistic assumption for this species: see

Caraco 1979). The second assumption implies that the observed dependence of scanning rate on group size is not merely a result of raptors preferring to attack very small flocks. For simplicity, I ignore occasional food-searching movements and aggression, so that a junco performs only two behaviors while foraging: scanning and pecking. The juncos' behavior is such that once a scan is begun, it is not repeated until the individual has pecked for food at least once. Any number of pecks may occur between scanning events. A single scan or peck is completed in about 0.7 s (Pulliam et al., in press).

Let "S" represent a scanning event, and let "P" represent a peck for food. Suppose that the internal process can be characterized as a first-order, discrete time Markov chain (e.g., Bailey 1964). That is, the probability that a given behavior will occur at time $t + 1$ depends on the behavior that the individual performs at time t and on no other behavior. Technical points useful in applying the theory of Markov chains to avian behavioral sequences have been discussed by Chatfield and Lemon (1970), Lemon and Chatfield (1971) and Thompson and Vertinsky (1975).

The Markov chain is defined, in part, by transition probabilities, $Pr(i|j)$. These are the conditional probabilities that behavior i will occur at time $t + 1$, given that the individual performs behavior j at time t. In this analysis, both i and j may be either S or P. the four transition probabilities of interest are:

$Pr(P|S) = 1$;
$Pr(S|S) = 0$;
$Pr(S|P) = \theta(n)$;
$Pr(P|P) = 1 - \theta(n)$.

A scan is always followed by a peck; $Pr(P|S) = 1$. After a peck, the bird may either scan or peck again. A peck is followed by a scan with a probability equal to $\theta(n)$; $0 < \theta(n) < 1$. A peck is followed by another peck with a probability equal to $1 - \theta(n)$. θ is depicted as a function of group size (n), since an individual's time budget depends on the size of the foraging flock. The model assumes that the individual selects a value of θ in response to an external variable, group size. Note that the transition probabilities are independent of time. Therefore, the model deals with a time-independent, or stationary, process and describes "steady state" behavior (Lemon and Chatfield 1971, Martindale 1980).

For any given group size, the model envisions an internal process which maintains a constant probability that a pecking bird's next behavior will be a scan, independently of the number of consecutive times the bird has just pecked. Effectively, the bird need not remember how many times it has pecked consecutively. It merely "tosses a coin" after each peck, and either scans or pecks again with respective probabilities of $\theta(n)$ and $1 - \theta(n)$.

Given this rather simple model for the sequential organization of an individual's behavior, one can predict the form of $f(L)$, the frequency distribution of pecking sequence duration. Clearly, the junco must peck at least once in each sequence. The probability that a sequence terminates after a single peck is:

$$Pr(L = 1) = Pr(S|P) = \theta(n).$$

The probability that a sequence extends for just two pecks is:

$$Pr(L = 2) = Pr(P|P) \, Pr(S|P)$$
$$= [1 - \theta(n)] \, \theta(n).$$

Continuing this line of reasoning, it becomes evident that the frequencies of pecking sequence durations will follow a geometric probability function. That is, the probability that a sequence is composed of exactly L consecutive pecks is:

$$f(L, \theta(n)) = [1 - \theta(n)]^{L-1} \, \theta(n)$$
$$L = 1, 2, \ldots$$

the expected (average) value of L is $[\theta(n)]^{-1}$. The single parameter of this distribution is $\theta(n)$, which is simply the probability that a bird scans following any peck.

Previous results (Caraco 1979) demonstrate that proportionately less time is spent scanning and more time is spent pecking as group size increases. To produce this pattern, a junco need only increase the mean number of pecks between scanning events as flock size grows. As the external variable (group size) increases, the individual could sense the change in its environment and reduce θ. The internal process remains a Markov chain, but θ should functionally depend on group size. If these considerations account for the overall time budgeting variation in scanning and pecking, I expect that:

1. The frequency distribution of pecking sequence lengths should be geometric for each flock size if the assumptions of the Markov chain are appropriate.

2. As group size increases, θ should decrease significantly. As a direct result, the mean length of pecking sequences will increase with group size.

The second expected result also follows from a consideration of the statistical equilibrium of a Markov chain (e.g., Bailey 1964). Independently of the initial behavior, a long sequence of pecking and scanning eventually will exhibit stable proportions of the two behav-

iors. At equilibrium, the proportion of pecks will be $[1 + \theta(n)]^{-1}$, and the proportion of scans will be $\theta(n)/[1 + \theta(n)]$. As $\theta(n)$ decreases, pecking increases and scanning decreases.

METHODS

I studied foraging flocks of Yellow-eyed Juncos in the Santa Catalina Mountains (near Tucson, Arizona) from January to April 1975 and from September 1975 to April 1976. Approximately 2,000 feet (about four h) of Super-8 movie film were taken of foraging groups ranging in size from one to five individuals. Average flock size at the study site varied from about 2.5 to 6 birds, and was inversely related to ambient temperature (Caraco 1979; see Ketterson 1978). Motion pictures were taken at 18 frames per second, and viewed at six frames per second. Scanning and pecking were easily discerned by viewing the films at reduced speed. A junco was considered to be scanning whenever it (1) cocked its head to the side, so that the upper eye could detect a predator's attack, or (2) lifted its head straight up, so that its bill broke a plane parallel to the ground at eye level. A peck was counted whenever the junco lowered its bill to the ground.

Film segments involving aggressive interactions were not included in this analysis. Aggression often resulted in a decrease in flock size (Caraco 1979). A departure from a group usually induced a temporary cessation of foraging by all flock members, violating the model's assumption of steady-state behavior. I sacrificed a bit of realism for the sake of simplicity by analyzing only sequences where flock size was constant and foraging was not interrupted by aggressive interference.

Films were taken between 12:00 and 13:00 on several days during each month of the study. Filming was confined to sites with relatively short grass. This insured that all individuals were visible and avoided any correlation between flock size and seed density within the data taken from the films.

RESULTS

The hypothesis of a Markov chain proposes that the length of pecking sequences will follow a geometric distribution. Table 1 presents the observed frequencies and expected theoretical distributions, for groups of 1 through 5 birds. Four of the five observed distributions are properly described by a geometric distribution (Chi-square analysis, see Table 1). The data for groups of four juncos, however, are clearly inconsistent with the geometric ($P < 0.005$). The observations for $n = 4$ were less variable than a geometric distribution with expected value equal to the observed mean duration. A
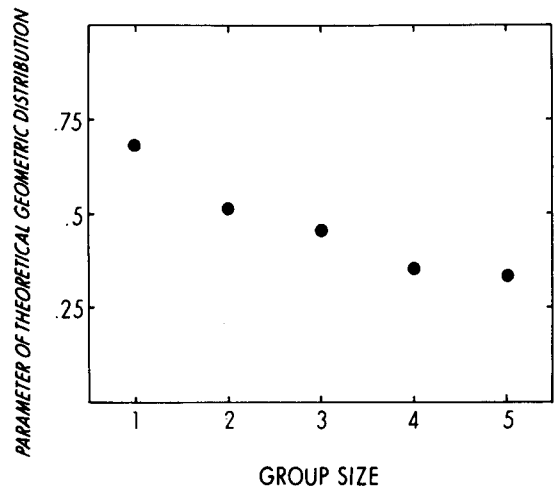

FIGURE 1.   Parameter of the theoretical geometric distributions, as a function of group size in foraging flocks of Yellow-eyed Juncos.

detailed analysis of the data for groups of four suggests that θ tended to increase as the number of consecutive pecks increased. In any case, since four of the five observed distributions were geometric, it may be acceptable to assume that the probability of scanning was constant after each peck, though this probability may depend on flock size.

The second hypothesis proposes that θ will decrease significantly as group size increases. If this is true, mean sequence length must increase with group size. Figure 1 shows $\theta(n)$, the parameter of the theoretical geometric distributions, as a function of group size. θ decreased significantly according to the linear regression:

$$\theta = .72 - .083 \text{ (Group size)} \qquad r = -.97.$$

Therefore, juncos must, on average, have pecked more often between scanning events as flock size increased. This relationship is given by:

Mean sequence length $= 1.12 + .38$
$$\text{(Group size)}$$
$$r = .96.$$

The form of the frequency distributions and the associated parameters generally support the simple hypotheses given above. Further, this analysis of behavioral sequences helps illuminate the observed positive correlation between feeding rate and group size found in this species (Caraco 1979).

DISCUSSION

Baker's (1973) concept of an internal stochastic process regulating the duration of a behavior, while responding to the environment through variation in its parameters, seems

TABLE 1. Observed distributions of the number of pecks per sequence and theoretical geometric distributions. Chi-square estimates indicate that four of the five observed distributions are satisfactorily described by the geometric. Only the distribution for flocks of four birds differs significantly from the theoretical.

Flock size = 1; mean length = 1.491, θ = .671; sample size = 715

L	1	2	3	4	5	≥6
Observ.	485	157	43	19	7	4
Exp.	479.8	157.8	51.9	17.1	5.6	2.8

$\chi^2 = 2.66$ $0.75 < P < 0.9$

Flock size = 2; mean length = 1.904, θ = .525; sample size = 387

L	1	2	3	4	5	6	7	≥8
Observ.	186	108	62	18	7	2	2	2
Exp.	203.2	96.5	45.8	21.8	10.3	4.9	2.3	2.2

$\chi^2 = 12.05$ $0.5 < P < 0.1$

Flock size = 3; mean length = 2.175, θ = .46; sample size = 263

L	1	2	3	4	5	6	7	8	≥9
Observ.	112	75	38	19	7	6	2	2	2
Exp.	121	65.3	35.3	19	10.3	5.6	3	1.6	1.7

$\chi^2 = 3.89$ $0.75 < P < 0.9$

Flock size = 4; mean length = 2.761, θ = .362; sample size = 209

L	1	2	3	4	5	6	7	8	9	10	≥11
Observ.	60	46	49	25	18	4	4	1	0	0	2
Exp.	75.6	48.3	30.8	19.6	12.5	8	5.1	3.3	2.1	1.3	2.4

$\chi^2 = 25.3$ $P < 0.005$ (reject)

Flock size = 5; mean length = 2.964, θ = .337; sample size = 165

L	1	2	3	4	5	6	7	8	9	10	≥11
Observ.	45	40	32	20	11	4	6	2	3	0	2
Exp.	55.6	36.9	24.4	16.2	10.7	7.1	4.7	3.1	2.1	1.4	2.8

$\chi^2 = 9.28$ $0.5 > P > 0.75$

plausible in light of the pecking duration distributions. First-order Markov chains may be reasonably appropriate for pecking and some bird song (e.g., Martindale 1980), but more complex sequences also may occur commonly. For example, the duration of behavioral sequences in foraging shorebirds (Baker 1973) and vocalizing Cardinals (Lemon and Chatfield 1971) sometimes show patterns more complicated than a first-order Markov chain.

My initial impression was that transitions between different neuro-muscular activities of a foraging granivore should depend on a complex array of internal and external stimuli, so that a simple Markov model would not sufficiently appreciate the behavioral complexity. However, the pecking sequence data are generally consistent with a first-order Markov chain, and they support Baker's hypothesized functional relationship to an important environmental variable (group size). Perhaps this level of analysis will help integrate neurophysiological and ecological approaches to avian decision-making.

ACKNOWLEDGMENTS

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