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SOME COMPONENTS OF FLOCKING BEHAVIOR IN THE ROCK DOVE (*COLUMBA LIVIA*)

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Abstract.—Observations of Rock Dove foraging behavior and estimates of individual vigilance indicate increased benefits for those birds in the center of the flock relative to those individuals on the periphery. Additional observations of reaction distances and responses to an approaching human also show increasing benefits for central Rock Doves as flock sizes become larger. Benefits to those birds on the periphery are less obvious, giving rise to several hypotheses regarding the determination of optimum flock sizes based on economic models of cost/benefit analyses and the adaptive value of flocking to those peripheral individuals.

ALGUNOS COMPONENTES DE LA CONDUCTA DE CONGREGARSE PALOMAS DOMÉSTICAS (*COLUMBA LIVIA*)

Sinopsis.—Observaciones sobre el comportamiento de forrajeo de la paloma doméstica (*Columba livia*) y estimados de vigilancia individual indican que hay un beneficio para aquellas aves en el centro de la parvada en referencia a las palomas que se alimentan en la perisferia. Otras observaciones relacionadas con la respuesta de las aves a un observador que se les acerca, muestran que a mayor tamaño del grupo, mayor el beneficio para las aves en el centro de la parvada. Los beneficios de las aves en la perisferia son menos obvios. Esto da origen a varias hipótesis en relación a determinar el tamaño óptimo de los grupos, basados en análisis de modelos costo/beneficio y el valor adaptativo de estar en la perisferia.

Studies on the value of flocking in birds have dealt primarily with the apparent contribution to the fitness of individuals through increased foraging efficiency and decreased predation. The former can be subdivided into benefits conferred by reduced search time (Krebs et al. 1972, Krebs 1974) and enhanced ability to flush prey items from hiding places (Morse 1970). The latter can be subdivided into increased effectiveness of surveillance for predators, "more eyes" (Bertram 1980, Powell 1974, Short 1961, Siegfried and Underhill 1975), decreased probability of predation on any particular individual, "the dilution effect" (Pulliam and Caraco 1984), difficulty encountered by predators in selecting and chasing a single prey individual within the flock, "the confusion factor" (Kenward 1978, Miller 1922), and the possibility of physical damage to a predator attempting to fly into a flock, "predator mobbing" (Tinbergen 1951).

This paper reports on field experiments designed to investigate the advantages and disadvantages associated with flocking in Rock Doves (*Columba livia*). It focuses primarily on the varying benefits accrued by an individual as a function of that individual's location in the flock, and the role of these benefits in the determination of optimal flock size. It also provides the opportunity for an empirical application of one theorem of Vine's (1971) model on the selective advantage of flocking which states: "The greatest individual security will be achieved by Q's (prey animals) which are inside the periphery of a solid circular flock."

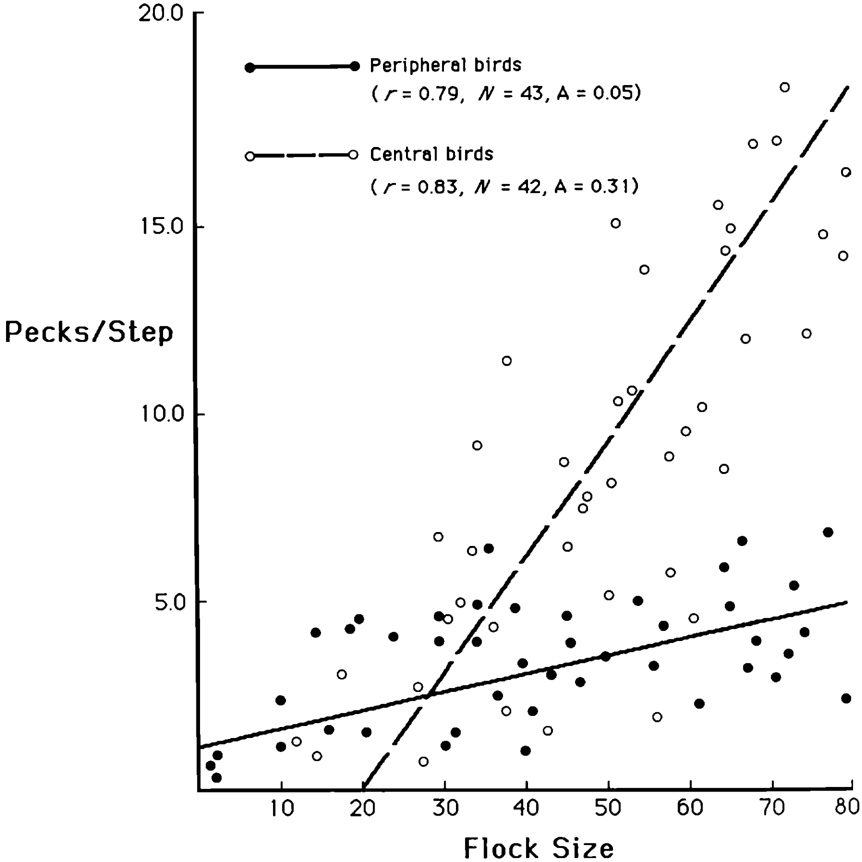

FIGURE 1. Flock size vs. pecks/step for centrally and peripherally located Rock Doves.

METHODS

Rock Doves, were studied in New Haven, Connecticut (elevation 50 m, latitude 41°15′N, longitude 72°55′W). The study site was an open, flat rectangular area 400 m long and 100 m wide. The sole vegetation was grass (predominant species were *Poa pratensis, Lolium perenne,* and several species of the genera *Festuca* and *Agrostis*). Data were collected from 29 September to 22 October 1985 between 0900 and 1100 h ("morning"), between 1230 and 1430 h ("afternoon"), and between 1600 and 1800 h ("evening"). Precipitation means for October and the whole year are 0.10 m and 1.20 m respectively. The temperature range for the data collection periods was 11 C to 21 C.

Flock size was determined by drawing an imaginary line around a group of Rock Doves so that all birds encircled by the line were within 2 m of another encircled bird while no bird that was not encircled was within 10 m of the line. All Rock Doves within the area were then counted. From a distance greater than 15 m, and for a period of 3 minutes, I counted the number of pecks at the ground and the number of steps taken by individual Rock Doves on the periphery, and alternately, in the center, of the flock. Peripheral birds were defined as those which were bordered on 3 or fewer sides by neighboring birds.

In the second part of the study, flock size was counted in a similar manner. A flock was then designated as "small" if it contained 6–15 individuals; "medium"—20–40 individuals; and "large"—more than 50 individuals. Data from flock sizes that did not fall into one of these categories were not used in this portion of the study. Individual Rock Doves on the periphery, and alternately in the center, of the flock were then selected randomly. The portion of the flock considered (center or periphery) was divided into 100 equal quadrats. A number between 0.00 and 0.99 was obtained from the random number generator of a Hewlett Packard hp15c hand-held calculator. This number was then multiplied by 100 with the product used to indicate the appropriate quadrat. The procedure was repeated until the quadrat selected was occupied by a bird. Starting from 20 m away, I walked toward the selected bird at 1.0 m/s. When the bird responded to my presence, I recorded the "reaction distance" between me and the bird and classified its response in one of the following categories: (1) walked away, continued feeding; (2) walked away, stopped feeding; (3) flew away, less than 10 m; and (4) flew away, more than 10 m. The direction from which I approached the bird was randomly chosen as follows: a number between 0.00 and 0.99 obtained from the random number generator of a Hewlett Packard hp15c hand-held calculator was multiplied by 360 with the product being used as the bearing from which the bird was approached. No further data were collected from a flock following its disturbance. Statistical methods followed Roscoe (1975).

RESULTS

Strong positive correlations occurred between flock size and pecks/step for individual birds in the center of a flock ($r = 0.83$, $N = 42$) as well as for birds on the periphery of a flock ($r = 0.79$, $N = 43$). Pecks/step values were obtained by dividing the number of pecks made in the observational period by the number of steps taken in the same period. The plot of these parameters (Fig. 1) illustrates the difference between the slopes of the regression line for central birds (A = 0.31) and that for peripheral birds (A = 0.05).

Strong positive correlations occurred between flock size and pecks/min for both central ($r = 0.77$, $N = 23$) and peripheral birds ($r = 0.78$, $N = 22$, Fig. 2). The central birds exhibited a greater rate of increase in pecks/min with increasing flock size (A = 0.78) than birds on the periphery of flocks (A = 0.40).

In small flocks, the mean reaction distances of peripheral birds ($\bar{x} = 3.74 \pm 1.34$ m) did not differ from the mean reaction distance of central

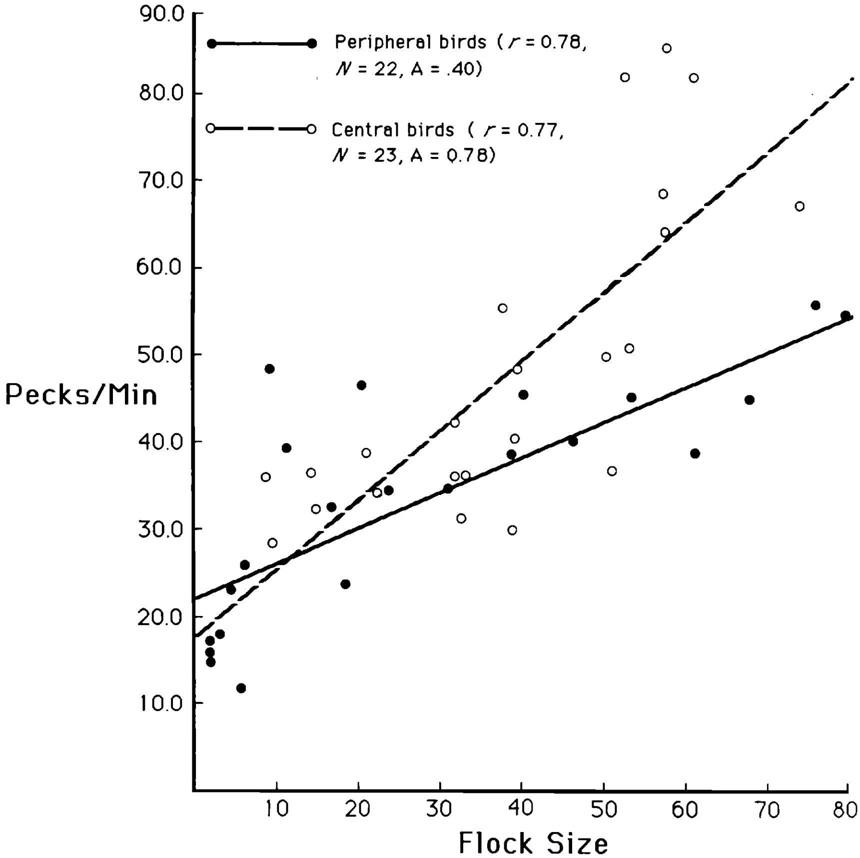

FIGURE 2. Flock size vs. pecks/min for centrally and peripherally located Rock Doves.

birds ($\bar{x}$ = 3.57 ± 1.80 m; t = 0.536, df = 48, $P > 0.05$) (Fig. 3). In medium-sized flocks, however, the mean reaction distance of central birds ($\bar{x}$ = 5.12 ± 1.49 m) was greater than that of peripheral birds ($\bar{x}$ = 4.02 ± 1.40 m; t = 3.804, df = 48, $P < 0.05$). In large-sized flocks the mean reaction distance of central birds ($\bar{x}$ = 6.68 ± 2.10 m) was also higher than the mean reaction distance of peripherally-located individuals ($\bar{x}$ = 3.98 ± 1.85 m; t = 6.822, df = 48, $P < 0.05$).

Among the central birds, there was an increase in reaction distance between small and medium flocks (t = 4.690, df = 48, $P < 0.05$) as well as between medium and large flocks (t = 4.284, df = 48, $P < 0.05$). An analysis of variance of the reaction distances of peripheral individuals in small, medium, and large flocks indicated they did not differ (F = 1.027, $P > 0.05$).

Of all birds approached, only those that reacted at a distance greater than 2.5 m were included in this study. This accounted for 90% of the

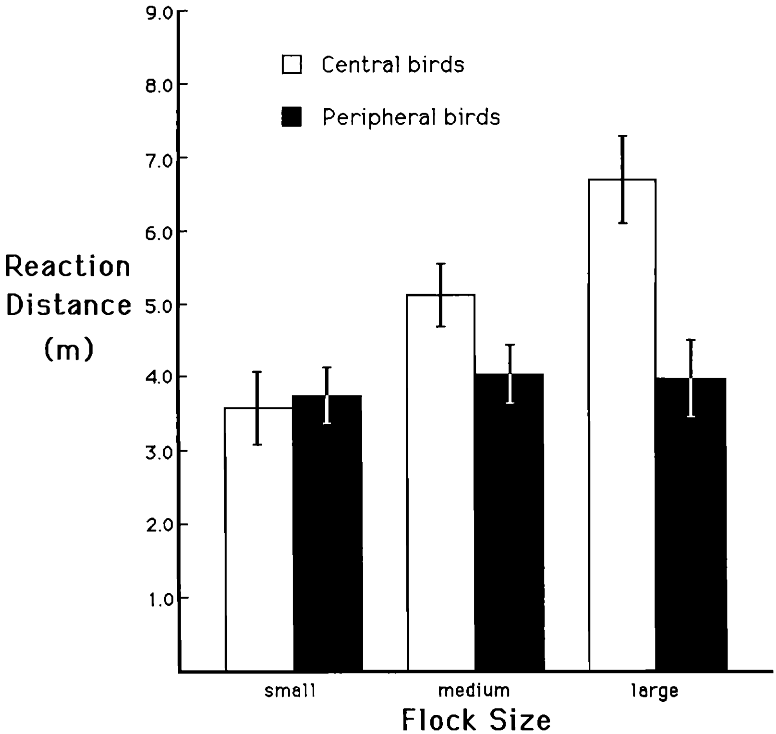

FIGURE 3. Mean reaction distances (±2 SE) of peripheral and central Rock Doves of small, medium, and large flocks.

total number of birds approached. Reactions of birds approached during the morning and afternoon differed markedly from the reactions of those approached during the evening (Fig. 4). Thirty-eight of 49 (78%) approached in the morning responded with reactions that were classified as response class (1) (walked away, continued feeding) or (2) (walked away, stopped feeding). Among the birds approached during the afternoon, 31 of 48 (65%) were of response class (1) or (2). In contrast, among birds approached during the evening, 36 of 50 (72%) responses were designated as response class (3) (flew away, less than 10 m) or (4) (flew away, more than 10 m).

DISCUSSION

This study supports the hypothesis that flocking increases the fitness of individuals that exhibit such behavior. Additionally, the individual benefits from flocking behavior vary as a function of the individual's location within the flock. Such variation may play a critical role in determining optimum flock size.

Increased foraging efficiency may be a result of flocking behavior (Fig.

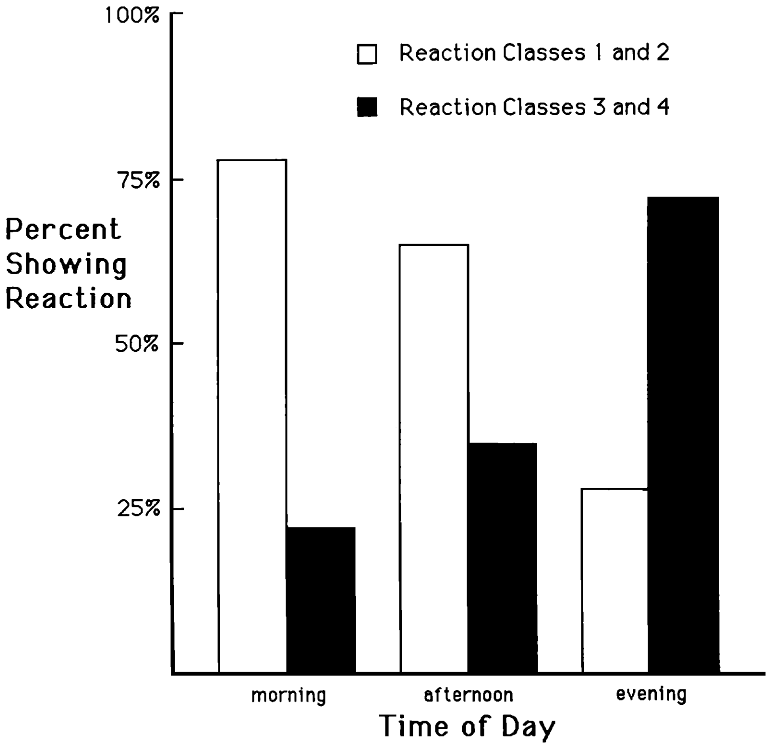

FIGURE 4. Percent of Rock Doves showing reaction class (1) and (2) or (3) and (4) during each of the observational periods. (See text for explanation of reaction classes.)

1) (Murton and Isaacson 1962, Murton 1971a, Murton et al. 1971). Using the measure pecks/step as an index of the relative food intake by birds in a given location, it is clear, considering the positive slope of both regression lines, that individuals in larger flocks are obtaining more food items/step than their counterparts in smaller flocks. Such a measure's validity as an index of relative food abundance rests in the assumption that with each peck an item of food is eaten. Observations indicate the assumption is true. One must be careful not to interpret such a measure as absolute caloric intake; it is a measure only of the relative quantity of food intake. Nonetheless, the difference suggests that with increasing flock size the benefits to birds on the periphery increase at a slower rate than the benefits to those birds in the flock's center. If the density of food decreases with distance from the center of the flock, there may be a critical density at which the costs associated with a highly visible flock are no longer offset by the benefits of the flock's enhanced foraging ability, thereby dictating the optimal flock size. In all flocks, one would expect to see the peripheral individuals feeding at the constant rate dic-

tated by the critical density. It was not possible to directly measure food densities; however, the positive slope of the pecks/step regression line for peripheral birds (Fig. 1) indicates that peripheral birds in smaller flocks take more steps, searching a larger area, in order to make the same number of pecks as peripheral birds in larger flocks.

Increased overall vigilance, with decreased individual vigilance is another frequently discussed potential advantage to a flock (Short 1961). To approximate individual vigilance, the measure of pecks/min was used. When it is not pecking at food, a bird may be actively looking for potential predators. Such an individual will notice a potential predator, whereas a bird that is pecking at a food item is unlikely to see a predator. Therefore, as pecks/min increase, an individual's vigilance decreases. Pecks/min increase with increasing flock size (Fig. 2). Such a relationship is easily explained by the idea that an individual's vigilance may decrease since that of the flock is increased as a result of "more eyes." Lazarus (cited in Dimond and Lazarus 1974) and Powell (1974) have shown that stimuli are detected sooner by large groups of birds than by smaller groups.

Because birds in the center of a flock are surrounded on all sides by neighbors while birds on the periphery are exposed on at least one side, it is not surprising that the pecks/min regression line (Fig. 2) for peripheral birds is below that of centrally-located birds. Peripheral birds spend more time looking and, hence, have less time to peck. Moreover, it is not surprising that the slope of the central bird regression line is greater than that of the peripheral bird regression line. Strictly from a vigilance point of view, increasing flock size should always benefit central individuals more than individuals on the periphery.

That birds inhabiting peripheral locations in the flock have lower feeding rates than other flock members has been firmly established (Murton et al. 1966, 1971; herein). Explanations of this discrepancy that rely on variable food densities and different vigilance needs, while accurate, may be incomplete. Additional factors probably help maintain the discrepancy. Observations by others (Murton 1971b, Murton et al. 1971) suggest that individuals occupying the periphery of a flock are low in the social hierarchy, while central individuals are dominant. Murton et al. (1971) found a correlation between the pecking rate of subordinate, peripheral birds and dominant, central birds. They explain this finding as being a result of the subordinate birds copying the feeding actions and rate of the rest of the flock. Consequently their pecking rate, which is low due to the bird's increased vigilance needs, is not correlated with the local food density.

Additional complicating factors introduced with social facilitation extend to the pecking rates of central individuals. Increased food intake as a result of socially facilitated group feeding has been shown in chicks (Matsuzawa and Horikoshi 1981) as well as black ducks and American coots (Penney and Bailey 1970). I am currently investigating this phenomena in Rock Doves.

When approached by a human, the reaction distance of Rock Doves increased in an almost linear fashion with increasing flock size (Fig. 3). Whether an individual bird perceived the approaching person as a threat or as a possible provider of food, they responded at greater distances in larger flocks.

No significant change was seen in the response distance of birds on the periphery with respect to flock size. This would seem to indicate a maximum benefit (with respect to reaction distances) that can be accrued by a Rock Dove that is in the periphery of a flock, whereas centrally-located Rock Doves would continue to benefit from the addition of individuals to the periphery of the flock. It appears that the optimal flock size must be dictated by the analysis of a situation of diminishing returns and increasing costs incurred by birds on the flock's periphery. These findings agree with those predicted by the theorem of Vine (1971) in that those birds on the periphery of a flock incur greater predation risks than centrally-located individuals due to a decreased reaction distance. Additionally, the peripheral birds incur a greater risk of insufficient nutritional intake due to their position being a greater distance from the highest density of food as well as having to devote more time to vigilance than pecking. The second of these risks plays a more significant role in habitats such as the Rock Dove's, which are often characterized by food coming from irregularly spaced "point sources" of food (i.e., humans).

A relationship was found between the nature of the Rock Dove's response to an approaching human and time of day. Most Rock Doves responded only by walking away from the human when approached in the morning or afternoon. However, when Rock Doves were approached in the evening, the vast majority responded with flight. These responses were consistent over the entire range of flock sizes as well as between peripherally and centrally-located birds. Kenward (1978) found a significant increase toward sunset in the crop contents of Rock Doves captured from flocks. Such a finding suggests that some type of cost/benefit analysis might occur in the determination by a Rock Dove of a response to the stimulus of an approaching person. The energetic cost of flying away exceeds the energetic cost of walking away. Perhaps what changes with time of day is the benefit that accrues to the bird by remaining in an area. In the morning, when nutritional needs are greater, the value of staying is relatively high. In the evening, though, with a full crop there is less to be gained by staying. Also, as Kenward (1978) suggested, at the end of the day Rock Doves may be more vulnerable through being less able to take off or maneuver rapidly than when their crops are not loaded.

Several benefits result from flocking, including increased foraging efficiency and increased vigilance. However, these benefits are not distributed evenly among all individuals in the flock. Instead, the benefits are less substantial for those individuals on the periphery of the flock than for those in the center. This recognition should permit a better understanding of the complex interactions of the many components that determine the optimal flock size in a given situation.

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