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Stability of Flock Composition in Urban Pigeons

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In temperate urban areas, feral Rock Doves (*Columba livia*) usually feed in flocks (Goodwin 1970). Although the term "flock" can be applied to avian groups that vary in their daily composition (Crook 1965, Morse 1980), it often is assumed that feral pigeon feeding aggregations that are fairly constant in size are made up of the same individuals from one observation to the next. Murton et al. (1972), for example, suggested that the composition of large pigeon flocks feeding on spilled grain in the port of Manchester is stable, but this may not be the case in habitats where pigeons depend on small, unpredictable sources of food. We conducted a study throughout the summer of 1984 on a small flock of urban Rock Doves in central Montréal, Québec to determine the stability of flock composition in this type of habitat. The study was done in the context of work on the cultural diffusion of a novel food-finding behavior (Lefebvre in press). For the cultural diffusion study, it was essential to know to what extent urban Rock Dove flocks are open or closed populations.

Forty-eight Rock Doves were captured with drugged seed (Thearle et al. 1971) at 0600 on 2 mornings in late May on a part of the McGill University campus where *C. livia* feed and roost (Lefebvre and Giraldeau 1984). Birds were marked individually with plastic patagial tags and numbered leg bands and released on the site 5 days after capture. Attendance counts of birds on the ground or roosting on adjacent buildings were conducted on 30 mornings (between 0800 and 0830) and 19 afternoons (between 1430 and 1500) at the site throughout June and July. Morning counts were made in conjunction with the cultural diffusion experiment, and food (a maximum of 140 g of mixed seed) was available at the start of each period. No food was provided by the observers for the afternoon counts. Birds were recaptured in mid-August on 2 mornings (0700), again using the drugged-bait method. With dosage levels that differed from those recommended by Thearle et al. (1971), i.e. 0.006 α-chloralose and 0.002 seconal by seed weight instead of 0.005 for both drugs, the survival rate of captured birds in our study reached 90–100%.

Of the 48 birds caught and marked in late May, only 23 (48%) remained on the site at the time of recapture 75 days later. Forty-five new birds attended the site in mid-August out of a total of 68 individuals caught in the recapture. This large change over time in the frequency of marked vs. unmarked birds was highly significant ($\chi^2 = 51.79$, df = 1, $P < 0.001$). On a day-to-day basis, the change in flock composition was reflected by a linear decrease in the average number of tagged birds seen both in the morning and in the afternoon counts (Fig. 1). Both counts showed very similar decreases in tagged-bird attendance despite the fact that provisioning occurred only in the morning. The decrease in attendance does not reflect progressive tag loss, because the daily departure rate obtained by attendance counts of tagged birds (0.200–0.215) was *lower* than the rate estimated from the capture-recapture data on banded birds: in the latter case, 25 banded birds would have been lost over 75 days, a rate of 0.333 individuals per day. This value falls just outside the upper 95% confidence limits of the slopes of the morning and afternoon regressions (morning 95% threshold value based on standard error of slope: 0.290; afternoon: 0.325). The decrease also cannot be attributed to an overall drop in flock size, which went from 20–25 birds in early June to 45–50 birds in late July.

Before tagged birds actually left the site, daily attendance was highly variable. Frequency of attendance can best be assessed by calculating the proportion of counts on which a given individual appeared before it was last seen, a measure that is unbiased by disappearance and by possible tag loss. For morning and afternoon counts, the distribution of daily attendance constancy was bimodal (Fig. 2): two-thirds of the birds appeared often on the site (on average, 72% of days for morning, 62% for afternoon), while one third were seen only rarely (on average, 13% of days for morning, 19% for afternoon). The two types of individuals can be referred

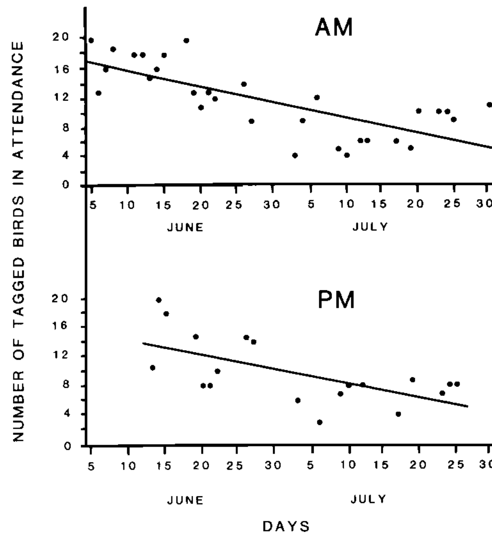

Fig. 1. Number of tagged birds in attendance on the morning (AM) and afternoon (PM) counts as a function of days. Linear regression for AM: $y = -0.215x + 17.171$, $r^2 = 0.551$, $F = 34.40$, df = 1,28, $P < 0.01$; for PM: $y = -0.200x + 14.021$, $r^2 = 0.401$, $F = 11.36$, df = 1,17, $P < 0.01$.

to as "regulars" and "occasionals." Regulars might be absent from the site for 1–11 observation days before being seen again (mean consecutive counts absent, morning: 2.30, SD = 2.08; afternoon: 1.79, SD = 1.10). The probability of observing the same regular on counts occurring on two consecutive days was 0.68 in the morning and 0.51 in the afternoon. That regulars returned to the site after 1 or 2 days' absence is reflected in the fact that the probability of seeing the same individual does not decay but remains relatively stable when counts are separated by 2 days (morning: 0.67, afternoon: 0.45), 3 days (morning: 0.67, afternoon: 0.34), 4 days (morning: 0.65, afternoon: 0.54), or even 5 days (morning: 0.63, afternoon: 0.45).

A subset of the attendance data, based on the 19 occasions when observations were taken both in the morning and in the afternoon, was analyzed in more detail for 18 individuals that were seen until the end of the study. Two of these birds were seen almost exclusively in the morning and 2 almost exclusively in the afternoon (individual χ^2 varied from 4.44 to 10.88, df = 1, $P < 0.05$ to <0.01). The other 14 individuals did not differ in morning vs. afternoon attendance, but did differ in their frequency of daily absence from the site: 5 birds were often away on both morning and afternoon counts (mean days absent: 11.60 out of 19), while 9 birds were seen regularly (mean days absent: 4.00; one-way ANOVA comparing days of absence for the two types of birds: $F = 43.51$, df = 1,12, $P < 0.001$). The 18 birds thus fall into 4 categories: whole-day regulars ($n = 9$), occasionals

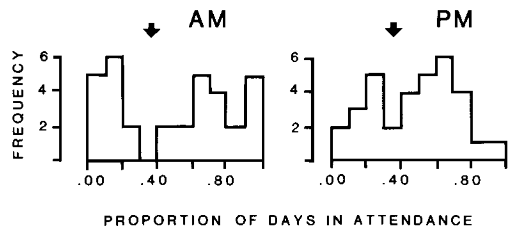

Fig. 2. Frequency distribution of individual site attendance regularity, expressed as the proportion of days an individual is seen on the site before it disappears. The arrows on the morning (AM) and afternoon (PM) diagrams represent the cut-off point (0.35) used to distinguish occasional and regular birds. n = 33 for both AM and PM.

($n = 5$), morning-only regulars ($n = 2$), and afternoon-only regulars ($n = 2$).

Co-occurrence of the 18 birds at the site was not random. The observed frequencies of co-occurrence for all possible pairs of birds were compared to expected frequencies generated by multiplying the occurrence frequencies of the individuals in each of the successive pairs. The distribution of observed co-occurrence frequencies differed significantly from the distribution of expected frequencies both in the morning and in the afternoon (morning: $\chi^2 = 30.81$, df = 9, $P < 0.001$; afternoon: $\chi^2 = 17.71$, df = 8, $P < 0.05$). In both cases, co-occurrence of regulars was greater than would be expected on a random basis, while co-occurrence of occasionals was lower than expected.

This study confirms the existence of individual differences in site use reported by Lefebvre and Giraldeau (1984). The results also suggest that small *C. livia* flocks in temperate urban areas may be considered open populations. Approximately one third of our birds were merely occasional visitors to the study site. Birds that remained on the site on a more regular basis were frequently absent and eventually left at a rate of 1 individual per 3–5 days. The presence of regular and floater individuals in avian flocks is well known in the genus *Parus* (Smith 1984). However, because urban pigeons may join several feeding aggregations in a day (Lefebvre and Giraldeau 1984), the presence of occasionals at our study site should not be considered as evidence for a floater "type" in feral *C. livia*. Birds that visited the study site only occasionally may have been regulars at another site. The frequent absence of regulars at our site is compatible with this view that urban pigeons sample different sites in adjacent areas. The distribution of birds among various feeding aggregation sites in an area may correspond to an ideal free distribution with frequent sampling of alternative sites (Fretwell and Lucas 1970). Urban pigeons have in fact been shown to adopt ideal free distribution patterns on a fine scale (Murton et al. 1972, Lefebvre 1983). Nesting schedules, either at the site or away from it, presumably interact with foraging to affect attendance patterns. For example, pairs of birds incubating eggs at a nest away from the study site would not visit the site together, a phenomenon that could be reflected in the fact that occasionals tend not to co-occur in attendance counts. Complete disappearance of a bird from the site is highly unlikely to be the result of mortality, since the study was done in the summer: food is often provided at the site in small and unpredictably variable amounts (Lefebvre and Giraldeau 1984), and factors such as disease, predation by cats, and collisions with cars cannot account for the progressive disappearance of 25 birds. In conclusion, this study suggests that urban pigeon feeding groups should not be seen as closed flocks, but as aggregations of individuals that sample many feeding sites and temporarily may adopt a particular site on a more regular basis.

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