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COMPETITION FOR FOOD IN URBAN PIGEONS: THE COST OF BEING JUVENILE[1]

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Abstract. The general-stated view that high mortality rates in young birds arises from a lack of behavioral proficiency is based on limited empirical evidence. The relationship between competitive foraging ability and age-specific mortality was examined in a free-ranging Rock Dove (*Columba livia*) population. In this system, competition for food was intense and predators were scarce. Young and adult pigeons showed considerable niche overlap, were members in the same flocks, and used similar foraging techniques, all of which favored competition between these age groups. Competition was especially intense when pigeons foraged on food provided by the public, which was the preferred and major food source for the population. Young pigeons were poorer competitors than adults in all situations analyzed. First, juveniles foraged less rapidly, and so were more vulnerable to exploitation competition. Second, juveniles were subordinate to adults within a despotic social system, and so suffered more from contest competition. These findings suggest that juveniles were less likely to attain a positive energy balance through the day and were more vulnerable to starvation and disease. As predicted, more juvenile corpses than expected were found during the study, indicating that young pigeons experienced higher mortality rates than adults. It is therefore suggested that differential mortality of juvenile and adult pigeons could in part arise from differences in competitive abilities over food.

Key words: age-specific mortality, Columba livia, *competition, foraging, Rock Dove, starvation, urban pigeons.*

INTRODUCTION

Birds of many species experience higher mortality in their first year of life than in subsequent years (Lack 1954). This age-specific mortality is an interesting assay in avian biology because of its implications for ecological and evolutionary theories (Grant and Grant 1989, Newton 1989). It often is stated that much of juvenile mortality arises from a lack of proficiency in behavioral traits such as foraging, avoiding predators, and interacting with competitors. For instance, the antipredator behavior of inexperienced juveniles may not be well developed, which would increase their vulnerability to predators (Lima and Dill 1990).

Starvation is one of the major causes of mortality in birds. Young birds are generally poor foragers when compared with adults (Marchetti and Price 1989, Wunderle 1991), and consequently may have difficulty in maintaining a positive energy budget throughout the day. The observation that young birds of some species suffer a decline in body mass soon after achieving independence points in this direction (Catterall et al. 1989, Sullivan 1989). Starvation can be a major factor implicated in differential mortality between juvenile and adult birds. To date, however, there are little data supporting a relationship between foraging success and age-specific mortality (Sullivan 1989).

The failure of juveniles to meet daily energy demands might arise not only from their lower foraging proficiency, but also from their lack of proficiency in competing with adults (Marchetti and Price 1989, Wunderle 1991). Competition may arise through depletion of food sources (exploitation competition, sensu Park 1962) or agonistic interactions (contest competition, sensu

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Nicholson 1954). The proximate consequence of both forms of competition is a reduction of a given individual's intake rate (interference, sensu Milinski and Parker 1991). The lack of juvenile proficiency in both foraging and competing compared with adults may act simultaneously in producing an unequal allocation of food between age-classes. The relative importance of each behavioral trait is probably related to the complexity of the foraging technique. Competition is expected to be relatively more important in those species in which foraging tasks do not require complex skills.

Rock Doves (*Columba livia*), being granivores, do not require complex foraging skills but must forage intensively (Johnston and Janiga 1995). Pigeons usually forage in groups rather than in cohesive flocks (Lefebvre 1985, Sol and Senar 1995). Individuals are able to store large quantities of food in their crops and need only a few minutes to fill the crop, which means that feeding rate is not limited by handling time (sensu Wunderle 1991). Thus pigeons can efficiently exploit ephemeral, abundant food sources, including those provided by the public or obtained by spillage in grain stores. Availability of these food sources has caused the excessive proliferation of pigeons in some urban areas (Murton et al. 1972a, Haag 1993, Johnston and Janiga 1995). By exploiting these ephemeral, abundant food sources, however, pigeons increase the level of intraspecific competition.

This paper explores the relationship between competitive foraging abilities and age-specific mortality in Rock Doves. Our pigeon population provided a good opportunity to investigate this topic because competition over food appeared intense and predators were scarce (Sol and Senar 1995, Sol, unpubl. data). Specific aims of this paper are to (1) study the opportunity for competition between age-classes in the study area, (2) analyze the age-related susceptibility to competition by exploitation or contest interactions, and (3) correlate age-specific foraging with mortality estimated by collecting pigeon corpses found in the same population.

METHODS

STUDY AREA

A free-ranging population of feral pigeons was studied in urban Barcelona, NE Spain, from October 1994 to February 1995 (see Sol and Senar 1995 for a map of the study area). Most data were recorded from a single population (referred to as RiT in Sol and Senar 1995), although data on feeding rate and social dominance also were collected from some peripheral populations. Predators able to capture pigeons were scarce in the area. In three years of field work, the only potential predators we observed were dogs, which rarely capture pigeons, and Yellow-legged Gulls *Larus cachinnans*. Yellow-legged Gulls were extremely scarce in the area and no attack was observed in all the time we spent in the field.

In the study area, pigeons were largely dependent upon two types of food sources: (1) sunflower seeds and pieces of bread provided by people (hereafter volunteer food) and (2) small particles of waste produced by human activity (waste food). These two renewable food sources differed in the way they were distributed in time and space. Volunteer food was provided by people in large quantities but available only for a short time in a limited area. Most of this food was provided daily at the same place and time by the same people. In contrast, waste food was available for a long time and widely dispersed but at very low concentrations. Consequently, exploitation of each type of food involved different foraging techniques. For instance, when foraging on volunteer food pigeons only needed to peck at food items, whereas when foraging on waste food pigeons also had to search for food items.

TRANSECT COUNTS

Study of foraging conditions and niche overlap between age-classes was carried out by means of transect counts. Niche overlap was assessed by the extent juveniles and adults differed in their use of the two types of food and how often they joined in mixed-age flocks. A route was selected such that all parts of the population's home range could be visited. The census took 30–35 min and was carried out 38 times, two censuses per day, from 07:00 to 10:00 each day. A mean (± SE) of 136.7 ± 11.5 pigeons per transect were observed feeding. For each observation we recorded, whenever possible, site, flock size, foraging density, age of individuals, type of food, and number of nonfeeding individuals. Individuals were aged using cere and iris color, which permitted discriminating juveniles at a distance (Kautz and Seamans 1986). A flock was defined as an aggregation of individuals with visual contact among them. Foraging density was estimated by dividing number of foragers by surface area occupied by the flock. Surface area was estimated from a circumscribed rectangle measured just after the flock had moved away. Each observation of a pigeon was assumed to be independent of others, because during the transects no pigeon movements were observed and hence the probability of counting an individual more than once was low. This assumption is further supported by the large size of the population, estimated as 1,130 ± 193 pigeons during the study period, and the low day attendance of individuals at the study area (Sol and Senar 1995).

FOCAL OBSERVATIONS

Age-related foraging abilities under exploitation and contest competition were assessed by measuring, respectively, feeding rate and social status of both young and adult pigeons. Information on foraging behavior for focal pigeons was recorded from 50 pigeon flocks from the main study area and surrounding areas. To avoid any disturbance, observations were carried out from a 30–40 m distance. Each flock was observed between 10 and 60 min, and many were recorded on videotape. For each flock, we recorded the behavior of 4 to 10 randomly selected pigeons, depending upon whether the flock flew away or not.

Because environmental variables such as type of food, site, or temperature could have influenced foraging rate, matched-pairs of observations of adult and juvenile pigeons were collected from each flock. We measured foraging abilities for the two main feeding techniques used by pigeons, exploiting volunteer food and searching for waste food. Feeding rate was measured by number of pecks made by an individual in 15-sec units of continuous feeding. We were unable to observe unsuccessful attempts due to the small size of some prey items. However, our observations of pigeons feeding on maize show that feeding rate and intake rate are positively correlated (r_{81} = 0.48, $P < 0.001$) and, hence, we assume that peck rate is a good estimation of intake rate (see also Phelan 1987). Focal observations in which the pigeon was involved in an agonistic encounter were excluded from the analyses.

Age-specific dominance status was assessed by analyzing the outcome of aggressive contests recorded during observations of pigeons foraging in groups. Most aggressive encounters were supplanting attacks. For each encounter we noted age of both winner and loser. An individual was considered to have won an encounter if its opponent withdrew. We also analyze direction of aggressive interactions in three video recorded flocks followed for as long as possible. Expected frequencies were calculated according to the proportion of each age-class observed in each flock and measured as the proportion of adult vs. juvenile pigeons recorded at the beginning and end of the monitoring time. For comparative purposes, we also recorded the number of interactions per 15 sec of adult-juvenile matched-pairs of observations of pigeons feeding on volunteer and waste food.

MORTALITY

Pigeon carcasses were often found during the field work. Every day spent in the field we actively searched for corpses within the population home range in the morning before the streets were cleaned. Data recorded from each corpse included: date, site, age, and apparent cause of death (road kill birds or other). Necropsies were not performed.

STATISTICAL ANALYSES

A Wilcoxon matched-pairs signed ranks test was used when comparing young and adult pigeons from the matched-paired focal observations. The other analyses were performed with Mann-Whitney U-tests. Tests of independence were performed with the χ^2-test. Values reported are means (± SE), unless noted otherwise.

RESULTS

USE OF FOOD RESOURCES

Volunteer food attracted larger pigeon flocks than human waste (Table 1). When both resources were simultaneously available, most pigeons (94.0 ± 3.5%) fed on volunteer food. Also, the percentage of birds feeding at a site was higher when volunteer food was available than when waste food was available (see Table 1). Although volunteer food was available for very short times, 37.5% of all pigeons observed during the transects foraged on this type of food. In addition to attracting more individuals, higher pigeon densities and rates of encounter also occurred when birds foraged on volunteer food

TABLE 1. Mean ± SE (n) foraging variables for volunteer and waste food. All P-values < 0.01 based on Mann-Whitney U-tests.

	Flock size	Density (birds m^{-2})	% pigeons feeding	Encounters per 15 sec
Volunteer food	50.6 ± 7.5 (44)	8.4 ± 1.1 (31)	76.9 ± 5.6 (20)	0.3 ± 0.4 (202)
Waste food	20.8 ± 2.5 (142)	1.5 ± 0.2 (47)	52.3 ± 3.8 (43)	0.1 ± 0.0 (122)

(Table 1). Juveniles and adults did not differ in the extent to which they used the two food sources ($\chi^2_1 = 0.6$, $P = 0.47$).

FLOCK FORAGING

Most pigeons were observed foraging in flocks (99.3% of observations). Mean size of 187 foraging flocks observed was 34.4 ± 3.3, with a maximum of 253 pigeons. Large flocks, composed of more than 80 birds, were frequently observed (Fig. 1A). The abundance of these large flocks may be accounted for by the large number of pigeons attracted to volunteer food.

Juvenile and adult pigeons usually were present in the same foraging flocks. Only in 24.4% of 180 flocks in which age-classes could be distinguished did we observe exclusively adult or juvenile groups. We do not attribute such age-specific groups to segregation between juvenile and adult pigeons into different flocks, but to the predominance of adults in the population. This attribution is supported by two observations. First, in only one occasion did we observe a group composed exclusively of juveniles, and this consisted of only two pigeons. Second, flocks formed exclusively of adults were small (9.30 ± 1.81) and hence likely formed adventitiously. Young and adult pigeons tended to forage in flocks of similar size (Fig. 1B), although juveniles were observed less than expected in the largest flocks ($\chi^2_1 = 12.8$, $P < 0.001$).

FEEDING SUCCESS

As expected, the peck rate was higher for pigeons feeding on volunteer food than it was for pigeons feeding on waste food (Table 2). However, adults showed a higher peck rate than juveniles in both situations. The disparity in juvenile/adult peck rate suggests that differences in peck rate between age-classes were higher when birds foraged on waste food than on volunteer food.

SOCIAL DOMINANCE

Adults were consistently dominant over juveniles. Of 200 attacks recorded, adults initiated 178 attacks (89%; $\chi^2_1 = 121.7$, $P < 0.001$) and won 184 (92%; $\chi^2_1 = 137$, $P < 0.001$). Juveniles were more likely to be involved in encounters than adults (Table 2). Three pigeon flocks were monitored for as long as possible to assess the directionality of the aggressive interactions between age-classes. Adults showed a tendency to direct more aggressions than expected toward juveniles but not to other adults (χ^2_1; in all cases $P < 0.02$). Juveniles initiated encounters on very few occasions.

MORTALITY

A total of 41 corpses was found during the study. Of these, seven corpses were excluded from analysis; one was a dead nestling and the rest were classified as road kills. Of the remaining corpses, 21 (62%) were juveniles. This percentage was significantly higher than expected by chance, according to a conservative estimate of 20% juveniles in the population ($\chi^2_1 = 35.3$, $P < 0.001$); the population was 12% juveniles based upon eight censuses conducted between October 1994 and January 1995. These results strongly suggest a differential mortality between adult and juvenile pigeons.

DISCUSSION

The main results of this study may be summarized in three points: (1) pigeons often foraged under high levels of competitive situations, (2) the foraging niche of juvenile and adult pigeons overlapped to a great extent, so both age-classes had to compete for the same resources, and (3) juveniles were worse competitors than adults in both exploitation and contest competition.

OPPORTUNITY FOR COMPETITION BETWEEN AGE-CLASSES

Pigeons showed a clear preference for foraging on food provided by the public rather than on waste food. This is not surprising because by selecting that food, pigeons achieved higher intake rates and obtained larger food items. On transects, the number of pigeons recorded feeding on volunteer food was not much lower than the number feeding on waste food, despite the short time volunteer food was available. This means that most food consumed by pigeons was provided by the public. In fact, the great quantity of food provided by the public is the likely cause of overpopulation of pigeons in the study area (Sol, unpubl. data).

The use of volunteer food resulted in high levels of competition between individuals. This type of food was an abundant, highly predictable resource, and pigeons often perched at roosting sites waiting until it became available. A large number of pigeons was attracted when the food became available, and it was depleted in a few minutes. This promoted the existence of scramble competition, a form of exploitation in which competitors exploit the same resource while seeing each other (Milinski and Parker 1991). Furthermore, foraging occurred at high densities and pigeons were often involved in agonistic encounters, promoting contest competition. The fact that the higher rate of encounters occurred while pigeons foraged on volunteer food supports the hypothesis that contest competition only appears when food is sufficiently abundant to compensate for the costs associated with such encounters (Wiens 1991).

Compared with volunteer food, waste food was exploited under low pigeon density, and encounters were scarce. Presumably, in this case, contest competition was not important. However, we cannot exclude the possibility that exploitative competition could operate, although it was much less apparent and probably less important than when pigeons foraged on volunteer food.

AGE-RELATED COMPETITIVE ABILITIES AND UNEQUAL RESOURCE PARTITIONING

A consistent foraging asymmetry was found: young pigeons were poorer competitors than adults in all situations analyzed. First, juveniles foraged less rapidly than adults, especially while searching for waste food. A lower foraging efficiency by juveniles has been previously reported for many other bird species and has been attributed to a lack of maturation of the nervous and muscular system as well as learning (see

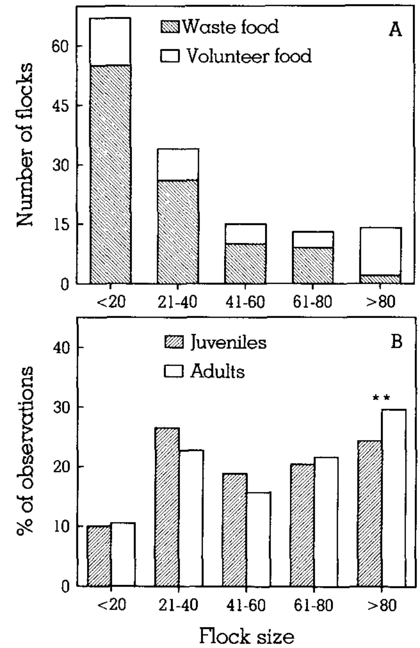

FIGURE 1. (A) Frequency distribution of foraging flock size in the study area. For each flock category, the proportion of flocks observed while feeding on volunteer and waste food also is shown. (B) Differences in flock size between juvenile and adult pigeons. More juveniles than expected were found in the largest flocks (**$P < 0.01$ with a χ^2-test).

Marchetti and Price 1989, Wunderle 1991). That young pigeons are slower foragers than adults means that they suffer more from exploitation competition. Consequently, it may be argued that juveniles could do better allocating more time to waste food and less to volunteer food, but we did not observe differences between age-classes in time allocated to each type of food. This might be due to the fact that human waste was a scarce resource and juveniles were relatively less efficient in exploiting it.

Second, our results showed a clear dominance-related system within the feeding flocks. Adult pigeons were socially dominant to juveniles, initiating and winning most encounters. Moreover, they showed a tendency to direct more aggression than expected toward juveniles. An explanation for this despotic behavior is that while juvenile pigeons represent a real foraging competitor for adults, there is little cost for adults in driving away juveniles.

TABLE 2. Foraging differences (mean ± SE [*n*]) between juvenile and adult pigeons feeding on volunteer and waste food. *P* is the probability associated to a Mann-Whitney *U*-test[a] or a Wilcoxon matched-pairs test[b]. Ratio is the peck rate disparity between juveniles and adults (juvenile/adult peck rates). Encounters by juveniles and adults while foraging on human waste were scarce, so the rate of encounters was not estimated in this case.

	Peck rate				Encounters per 15 sec		
	Juveniles	Adults	P^b	Ratio	Juveniles	Adults	P^b
Volunteer food	29.9 ± 0.9 (85)	36.9 ± 0.9 (85)	<0.001	0.82 ± 0.02 (85)	0.24 ± 0.05 (100)	0.13 ± 0.03 (100)	<0.001
Waste food	11.4 ± 1.2 (40)	16.7 ± 1.5 (40)	<0.001	0.73 ± 0.05 (40)	—	—	
P^a	<0.001			<0.001	—	—	

FLOCKING, COMPETITION, AND SPATIAL DISTRIBUTION

Pigeons generally were observed foraging in flocks. Advantages of flocking include, among others, enhancement of foraging efficiency and predator avoidance (Krebs and Davies 1993). However, flocking also may involve costs, the most obvious being competition. Because the benefits derived from cooperation increase at a diminishing rate compared with the cost of competition, above a certain flock size the benefits per individual decrease as more members join the group (Zemel and Lubin 1995). In our study area, pigeons often had to forage in large flocks, especially when they foraged over volunteer food. Dominant birds may not be able to avoid other individuals joining them in the flock, especially when the number of newcomers is large. In large flocks the cost of competition was probably higher than potential benefits, especially when taking into account the absence of predators and the predictability of most food sources. This suggests that pigeons were forced to forage in flocks that were larger than the optimal size. It is therefore likely that competition affected all individuals in the flock, although the consequences were more dramatic for poorer competitors.

Young pigeons tended to be under-represented in the largest flocks. This may be interpreted as a tendency to avoid larger flocks and hence the most competitive situations. Avoidance of larger flocks could explain why juveniles tend to forage in the suboptimal feeding sites (Sol, unpubl. data).

UNEQUAL RESOURCE PARTITIONING AND MORTALITY

Our data suggest that juvenile pigeons suffered higher mortality than adults. Other studies have shown similar results (Murton et al. 1972b, Kautz 1985). Although this is a general pattern among birds (Lack 1954), the reason for such age-dependent mortality has rarely been demonstrated (Catterall et al. 1989, Sullivan 1989).

Because necropsies were not performed, we do not know the actual causes of death. However, in our case, predation was negligible as few predators occurred in the area. The few observations of road kill birds also suggest that accidents were of little importance. On the other hand, our findings that young pigeons were competitively inferior to adults and had to compete with them for food suggest that resources were unequally allocated between age-classes. This means that juveniles were probably in worse physiological condition than adults and consequently more prone to starvation and disease. Estimates of body condition in pigeons from a nearby population (Sol, unpubl. data) supports this idea: juveniles showed a lower body condition compared with adults. The risk of starvation generally is thought to be higher when animals live in unpredictable environments (Krebs and Davies 1993). Instead, our pigeon population exploited resources highly predictable in time and space. However, we think that this does not contradict the above idea. In our case, competition may add uncertainty concerning the quantity of food that can be obtained by poorer competitors. We therefore suggest that a lack of competitive proficiency in foraging could explain in part why young pigeons experience higher mortality than adults. However, juveniles could be dying for reasons other than their inability to get enough food, but these other reasons were not assessed in this study. In consequence, further studies should determine whether starvation is the only factor implicated and, if not, what is its relative importance in the differential mortality of juveniles.

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