THE EFFECT OF EXTRA FOOD ON FITNESS IN BREEDING CARRION CROWS[1]

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Abstract. Food limitation during the nestling stage was experimentally investigated in an urban population of Carrion Crows. Parents were offered supplemental food during the nestling period and the following variables compared with those from non food-supplemented pairs: (1) nesting success, (2) fledgling number, (3) fledgling mass and linear body size, (4) proportion of fledglings resighted (a) after transition to independence from the parents, and (b) after the first winter postfledging, and (5) the probability that a fledgling became a breeder. Food-supplemented pairs had a higher nesting success and produced more fledglings. The fledglings of food-supplemented pairs were heavier and bigger in tarsus length than controls, but experimental and control fledglings were seen in equal proportions both after transition to independence and after the first winter. The production of potential breeders was increased ninefold in food-supplemented pairs. The study demonstrates that in this urban habitat food limitation causes low fitness not through lowered survival, but through the production of a low number of potential breeders.

Key words: body mass; Carrion Crow; Corvus corone corone; *food limitation; food supplementation; linear body size; nesting success; nestling phase; resightings; survival; territory acquisition.*

INTRODUCTION

In a review of the effects of food limitation on reproductive success and survival of birds, Martin (1987) considered food limitation within the context of life history theory. He pointed out that in most of the studies reviewed, an evaluation of postfledging survival of the offspring is lacking. Obviously this is one of the most important parameters needed to evaluate food limitation during breeding in a fuller life history and evolutionary perspective. Further, Simons and Martin (1990) showed that in most experimental studies of food limitation and avian reproduction, the birds were supplemented with food during several stages of the reproductive cycle at a time, e.g., prelaying, nest building, egg laying, incubation, nestling, and fledging phase. Thus the consequences of food limitation during one stage could not be separated from those during earlier stages. They pointed out the lack of experimental studies concerning the question of food limitation during the nestling stage alone and studied the effect of limited food on present and future reproduction in the Cactus Wren (*Campylorhynchus brunneicapillus*) during this stage. Their findings demonstrated that nestlings in food-supplemented nests had greater mass and linear dimensions and a higher postfledging survival than controls.

In general, food limitation during the reproductive phase can limit fitness by reducing the number of offspring fledged, the quality of the fledglings, or both. Lower quality fledglings may show lower fledging mass and smaller tarsus length, a measure corresponding to linear adult size in many passerines (e.g., Garnett 1981, Alatalo and Lundberg 1986, Møller 1989, Richner 1989a, but see Smith et al. 1986). Fledging mass is often correlated with postfledging survival (e.g., Perrins 1965, Moss 1972). Two periods are critical for survival, the transition to independence (i.e., ≈3 mo in the present population) and the first winter after fledging. Linear size may determine social status (Searcy 1979, Garnett 1981, Clutton-Brock et al. 1982), which can itself influence survival (e.g., Fretwell 1969, Kikkawa 1980, Arcese and Smith 1985). Further, linear size can limit the access to breeding resources (Alatalo and Lundberg 1986, Richner 1989a). It seems therefore important to assess experimentally, during the nestling period, the effects of food limitation on fledgling number, fledgling mass, and linear size, and to investigate the consequences for survival and acquisition of breeding resources.

My previous studies on a large population of individually marked Carrion Crows (*Corvus corone corone*) provided a background to this study. In particular, I showed that most urban fledglings are smaller in linear body dimensions than rural fledglings, and are consequently excluded from territory acquisition and hence reproduction (Richner 1989a). Further, there is a positive correlation between linear body size and social status (Richner 1989b, Richner et al. 1989), and between linear body size and access to food (Richner 1989b). There is no significant difference in linear body size between rural and urban breeders (Richner 1989a). Here I analyze, in a high density urban population of Carrion Crows, the effect of extra food during the nestling phase on: (1) nesting success, (2) fledgling number, (3) fledgling mass and linear size, (4) the probability of

resighting a fledgling after the period of transition to independence from the parents, and after the first winter postfledging, and (5) the probability of a fledgling becoming a breeder.

METHODS

The study population.—An urban population of Carrion Crows was studied between 1985 and 1989 in Lausanne, Switzerland. This population presents the highest density of breeding territories recorded for the species. The core (0.86 km²) of the study area held 32 pairs, which gives a density of ≈36 pairs/km². Four of these breeding pairs had helpers at the nest over one or several years (Richner 1990). The territories are defended year-round. Large flocks of nonbreeders live in parts of the study area that are less suitable for breeding.

Experimental and control birds.—From 1986 to 1989 extra food was given to a total of 11 randomly selected pairs (3 pairs in 1986, 2 in 1987, 5 in 1988, 1 in 1989) during the period between hatching and fledging of the chicks. The food consisted of ground beef, fish, and raw eggs. Approximately 500 g of this mixture were placed on the ground at the center of each pair's territory between 0700 and 1000 every day. Food was consumed or stored by the territory owners within <20 min of provisioning. All birds were kept under survey during that time and no other animals than the territory owners were seen consuming the provided food. During the same years a total of 84 pairs with nests containing hatched young (18 pairs in 1986, 17 in 1987, 20 in 1988, 29 in 1989) served as controls. These nests were followed until the chicks died or fledged. A nest was considered as successful if at least one of the hatchlings later on fledged; henceforth the term nesting success is used to describe whether or not a nest that had hatching eggs produced at least one fledgling. Three fledglings of the food-supplemented group wandered off the branches when we approached the nest and could not be caught. However, since they fledged they were retained for the calculation of nesting success but discarded from all the other analyses. Eleven fledglings were taken in captivity for dominance tests. A total of 82 fledged birds were used for evaluating postfledging survival.

Measuring of birds.—All fledglings were weighed at an age of 30–34 d and the tarsus length, beak dimensions, and wing length measured. As shown elsewhere (Richner 1989a, b), body mass and tarsus length stabilize by that age. The sex of the fledglings was determined by laparoscopy (Richner 1989c).

The breeders were caught in a large wire-mesh trap or by the use of a stupefying bait. Mass, tarsus length, wing length, and beak dimensions were recorded, and their sex determined by laparoscopy. The birds were wing-tagged and released within a few hours after capture, and all birds took their territory up again after the procedure.

Tarsus length of a fledgling is strongly correlated with other linear measures of body size and hence can be taken as a representative measurement of overall body size (Richner 1989a). Further, as in many other passerines, there is no postfledging tarsus growth in the Carrion Crow, and fledging size thus equals adult size (Richner 1989a).

Resighting and survival.—One assumption made in this study was that birds in the supplemented and the control group have an equal chance of being resighted after fledging. Although resighting a bird implies its survival, no resighting does not mean that the bird died, since it could have dispersed and survived elsewhere. In order to use the proportion of birds resighted as a measure of survival it must be assumed that the provisioning of additional food does not influence postfledging dispersal. This assumption was evaluated by regularly searching the area within a radius of 25 km of the breeding site for marked birds. However, all resightings of previously marked fledglings ($N = 82$) occurred within a radius of <11 km from their original breeding site. A comparison of the distances of the last sightings to the original breeding site of the birds from the food-supplemented (mean [±1 SD] resighting distance = 1.8 ± 2.4 km) vs. the control birds (1.2 ± 2.1 km) shows no difference in resighting distances between the two groups (Mann-Whitney U test [with ties present in data], $z = 1.32$, $N = 45$, two-tailed $P = .19$). Hence, I believe that food supplementation did not affect dispersal and that all birds had an equal chance of being resighted after fledging.

RESULTS

The effect of extra food on nesting success

In all 11 nests where food was provided during the nestling period, the parents succeeded in fledging at least one chick. Only 33 of the 84 control nests (i.e., 39%) that contained hatched eggs fledged at least one chick. The difference in nesting success between experimental and control nests is highly significant ($\chi^2 = 14.4$, df = 1, $P < .001$).

The effect of extra food on the number of fledglings

The parents of all control nests, including the 51 nests where chicks hatched but none fledged, produced on average 0.77 ± 1.11 fledglings (mean ± 1 SD, $N = 84$), whereas the parents of the experimental nests raised on average 2.82 ± 1.08 chicks ($N = 11$) successfully. Thus, by providing extra food two more fledglings were raised per nest. This difference is highly significant (Mann-Whitney U test, $z = 4.63$, $N = 95$, $P < .001$).

The effect of extra food on fledgling body mass and size

The Carrion Crow is a sexually dimorphic species and hence the effect of extra food on fledging body

TABLE 1. Size (body mass and tarsus length) of fledgling Carrion Crows for a group raised by their parents under natural conditions and for another one provisioned with extra food between hatching and fledging.

	Mass (g)			Tarsus length (mm)		
	Mean	SD	N	Mean	SD	N
Males						
No extra food	381.0	41.9	31	65.5	2.5	33
Extra food	436.2	30.5	14	68.2	1.4	14
Females						
No extra food	342.8	40.3	32	62.7	3.7	32
Extra food	377.3	20.7	13	64.9	1.2	14

FIG. 1. Distribution of male fledglings by fledging mass for food-supplemented birds (dark stippled bars) ($N = 14$), and for controls (light stippled bars) ($N = 31$).

mass and size was analyzed separately for males and females. The mass of chicks receiving extra food was significantly higher at fledging than that of the controls for both males ($t = 4.42$, df $= 43$, $P < .001$) and females ($t = 3.77$, df $= 40.3$, $P = .001$) (Table 1, Figs. 1 and 2). Similarly there was a significant increase in tarsus length of both males ($t = 4.77$, df $= 40.9$, $P < .001$) and females ($t = 2.96$, df $= 41.6$, $P = .005$) when extra food was provided during the growth period (Table 1, Figs. 3 and 4).

The effect of extra food on survival of fledglings

Males and females were resighted in equal proportions 3 mo after fledging, i.e., the period of transition to independence (Table 2A; log-likelihood ratio test, $G = 0.649$, df $= 1$, $P > .4$), and after the first winter postfledging (Table 2B; $G = 0.454$, df $= 1$, $P > .5$). Data for males and females were therefore pooled for the analysis of resightings with respect to provisioning of food. A comparison between the proportion of birds of the extra food vs. the control group resighted 3 mo after fledging shows that extra food had no effect on the probability of being resighted (Table 3A; $G = 0.00134$, df $= 1$, $P > .9$). Similarly, there was no effect on resighting probability after the first winter (Table 3B; $G = 0.196$, df $= 1$, $P > .6$). Assuming that all birds had an equal chance of being detected after fledging, there is neither a significant effect of extra food on survival to independence from the parents, nor on survival through the first winter after fledging.

The effect of extra food on the probability of becoming a breeder

The acquisition of a breeding territory with respect to experimental and control group could not, in such a long-lived species, be tested directly during the time of the present study. However, there is a minimal linear body size required to acquire a breeding territory and therefore breeder status (Richner 1989a). In both the rural and the present urban population this critical size was found (Richner 1989a) to be 68 mm in tarsus length for breeding males (i.e., 93.3% of all known male breeders) and 65 mm for breeding females (i.e., 92.7%
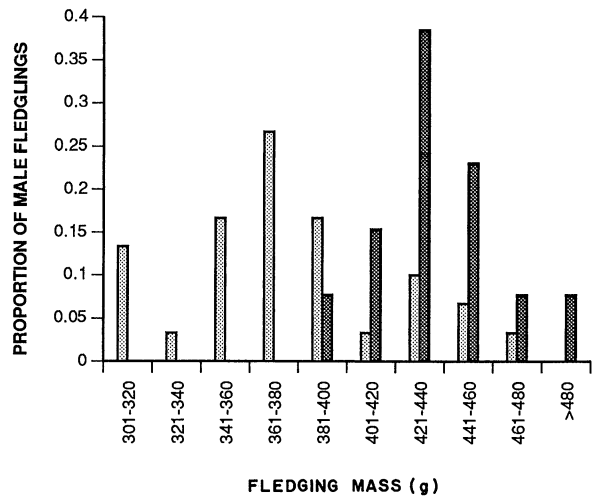
of all known female breeders). For both males and females there was no significant difference in mean tarsus length between urban and rural breeders. Since tarsus length remains stable after fledging and is a representative measure of overall body size (Richner 1989a), the proportion of fledglings of this critical body size or larger was compared between food-supplemented pairs and controls (Figs. 3 and 4). A significantly higher proportion of the food-supplemented fledglings was above that critical size than fledglings of the control group (Table 4; log-likelihood ratio test, $G = 8.833$, df $= 1$, $P < .003$).

The fitness of experimental pairs vs. controls

For the calculation of a fitness-correlated parameter of breeders under the two food conditions, the mean
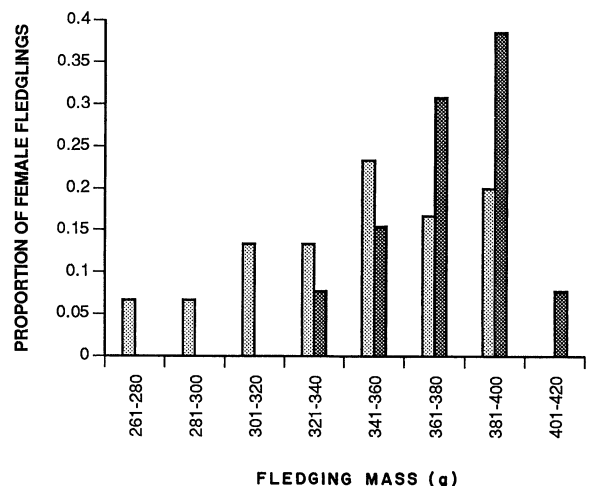

FIG. 2. Distribution of female fledglings by fledging mass for food-supplemented birds (dark stippled bars) ($N = 13$), and for controls (light stippled bars) ($N = 32$).
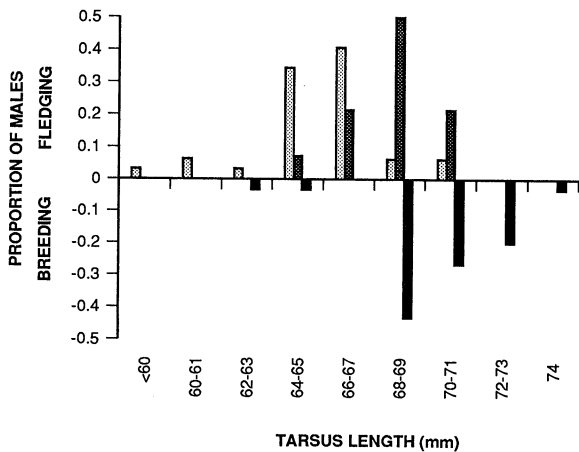
FIG. 3. Distribution of male fledglings by tarsus length for food-supplemented birds (dark stippled bars) ($N = 14$), and for controls (light stippled bars) ($N = 33$). The inversed black bars show the distribution of male breeders ($N = 30$).
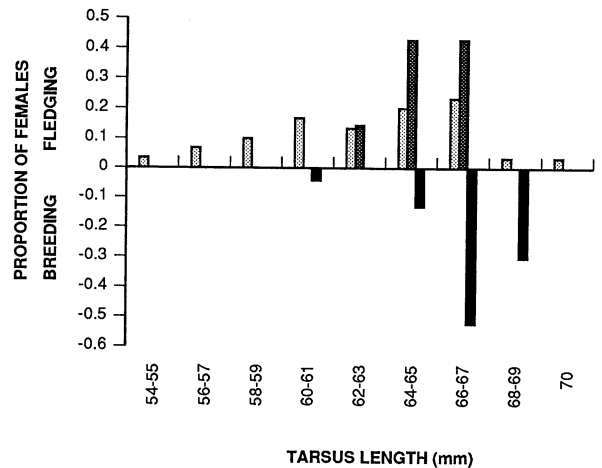

FIG. 4. Distribution of female fledglings by tarsus length for food-supplemented birds (dark stippled bars) ($N = 14$), and for controls (light stippled bars) ($N = 32$). The inversed black bars show the distribution of female breeders ($N = 23$).

number of chicks fledged per nest by each treatment group was multiplied by the proportion of fledglings above the critical body size necessary for becoming a breeder (Table 4). For the controls this calculates as 0.19 chicks per pair (i.e., 0.77 fledglings × 16/65), whereas for food-supplemented pairs this calculates as 1.81 chicks per pair (i.e., 2.82 fledglings × 18/28). The production of fledglings that are potential breeders is therefore more than nine times as high for the pairs provided with extra food during the nestling stage as for the controls.

DISCUSSION

Yom-Tov (1974) supplemented breeding Carrion Crows in rural areas in northeastern Scotland with additional food from the time of laying the first egg until fledging. Birds that had access to surplus food raised more, but not heavier, fledglings than control birds. There was no difference in clutch size, and thus the higher number of fledglings was due to lower chick mortality in food-supplemented nests. However, extra food did not influence fledging mass. In the present study extra food influenced both fledgling number and fledging mass. In order to interpret the difference in the findings of the two studies, it is interesting to note that the food-supplemented birds in the present study reached a fledging mass similar to the one recorded for fledglings in an adjacent rural area without addition of

food (Richner 1989a), and that this fledging mass was still below that recorded by Yom-Tov in both his experimental and control birds. Linear size of offspring was not measured in Yom-Tov's study but given the rapid growth and high fledging mass of both experimental and control birds, it is likely that there was no difference between the two groups in his study. Thus, the difference between the two studies may indicate that in Yom-Tov's study the fledging mass without additional food was already close to an optimal level, and that in my study population, food limitation is a more restraining factor for reproduction.

Compared with the urban population (36 breeding pairs/km²) studied here, both Yom-Tov's population (4 breeding pairs/km²) and the rural population (6 breeding pairs/km²) that I studied previously (Richner 1989a) are at much lower density. Yom-Tov (1974), in a second experiment, supplemented birds in 10 adjacent territories with food between 1 January and egg laying. Breeding density did not increase as an effect of food addition and he suggested that food abundance was not the ultimate factor determining breeding density. In my study, the breeding density of 36 pairs/km² did not decrease between 1984 and 1990, despite the low reproductive output. In the adjacent rural area the breeding density was only 6 pairs/km², and reproductive output was significantly higher (Richner 1989a).

TABLE 2. Contingency tables for testing the independence of sex and (A) resightings after the period of transition to independence, (B) resightings after the first winter postfledging.

	A) 3 mo postfledging			B) After first winter		
	Not resighted	Resighted	Total	Not resighted	Resighted	Total
Males	14	21	35	19	16	35
Females	23	24	47	29	18	47
Total	37	45	82	48	34	82

TABLE 3. Contingency table for testing the independence of food provisioning and (A) resightings after the period of transition to independence, (B) resightings after the first winter postfledging.

	A) 3 mo postfledging			B) After first winter		
	Not resighted	Resighted	Total	Not resighted	Resighted	Total
No extra food	27	33	60	36	24	60
With extra food	10	12	22	12	10	22
Total	37	45	82	48	34	82

This may indicate that population density is not influenced by reproductive performance, but rather determined by other factors such as the defendability of the territory, the vegetation structure (Smith and Shugart 1987, but see Ewald et al. 1980), the intruder density (Myers et al. 1979), or the distribution of food as suggested by Yom-Tov (1974). Although the present study shows that food limits reproductive performance in this urban, high-density population, food availability is probably only a proximate cause, and the ultimate cause may be found in one or several of the factors that limit population density.

A question often raised in avian reproduction is whether number or quality of offspring is optimized (e.g., Smith and Fretwell 1974, Brockelman 1975, Myers 1978, Winkler and Wallin 1987). This poses the problem of how quality of offspring can be assessed. Obviously a high-quality offspring is one that leaves a large number of grandchildren to its parents. To achieve this there are two important steps: first, an offspring must survive to breeding age, and second, it must then be able to acquire the necessary breeding resources, i.e., a territory and mate. Most food-supplementation studies consider only the survival of individuals (i.e., the first step) and do not evaluate their breeding potential (i.e., the second step). Since it has been shown in some species that survival is dependent on fledging mass (Perrins 1965, but see Nur 1984), it is often assumed that fledging mass adequately represents the quality of offspring. This study, however, shows that fledging mass is an inadequate measure of quality in the Carrion Crow (i.e., light and heavy fledglings survived equally well to the age of independence from the parents and to the end of their first winter) and that linear size is the more important measure since it is correlated with the probability of becoming a breeder. Thus, in some species, as in Carrion Crows, selection acts more strongly on the second step, whereas in other

species survival to breeding age might be the most critical period.

In conclusion, in Carrion Crows, food limitation during the nestling stage affects fitness by influencing nesting success, fledging number, and linear fledging size. Fledgling size is important since natural selection acts on linear body size rather than on body mass and survival. Both the number and quality of offspring can be affected by the food levels during the nestling stage.

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TABLE 4. Contingency table (both sexes combined) for testing the independence of food provisioning and the empirically established critical size limit for becoming a breeder (68 mm in tarsus length for males, 65 mm for females).

	Below size limit	Above size limit	Total
No extra food	49	16	65
With extra food	10	18	28
Total	59	34	93

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