

CORRELATES OF REPRODUCTIVE SUCCESS IN COOPERATIVELY BREEDING WESTERN AMERICAN CROWS: IF HELPERS HELP, IT'S NOT BY MUCH¹

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Abstract. I measured annual reproductive success for a resident population of cooperatively breeding Western American Crows (*Corvus brachyrhynchos hesperis*) over 6 years, and examined the relationship between it and several ecological and social variables. Most nests (57%) failed to fledge any young, due largely to predation. Success in fledging young was associated with three interrelated variables: (1) the presence of helpers, (2) early nesting, and (3) consistent differences between pairs. Assisted pairs began incubation earlier, some pairs consistently nested early, and the proportion of years that pairs were successful was related to the proportion of years in which they had help. Although both help and incubation date were related to nesting success independent of each other, the effect of help became nonsignificant after controlling for differences between pairs. The slight increase in fledging success possibly attributable to helpers may have been the result of consistently successful pairs succeeding, with help, in otherwise poor years. Postfledging survival was related in part to the size of individuals; larger nestlings tended to have a greater chance of fledging, and once fledged, to have a greater chance of surviving the following 2-week period. Larger nestlings survived to one year of age significantly more often than smaller nestlings.

Key words: American Crow, cooperative breeding, *Corvus brachyrhynchos*, incubation date, pair quality, predation, reproductive success.

INTRODUCTION

Over the last 20 years, many studies of cooperatively breeding birds have focused on the search for adaptive explanations for helping behavior, and many of those studies have demonstrated that the presence of helpers correlates with an increase in the breeding success of assisted pairs. Yet such observations do not necessarily point to helpers as being responsible for the increased success, because helper presence may covary with other characteristics of pairs that affect success, such as territory or pair quality (Brown 1987, Koenig and Mumme 1990, Emlen 1991). Various approaches have been used in attempts to resolve this issue, including: (1) measuring the effect on breeder reproductive performance of removing helpers or manipulating other variables presumed to affect success, (2) assessing the effect of help as distinct from group size via "natural" and manipulative experiments, (3) using multivariate statistical analysis to tease apart the effects of helpers on breeding success from those of other factors, and

(4) comparing the success of the same pairs in years with and without help (Cockburn 1998). I used the latter two approaches to analyze the effects of helpers and several other variables on annual reproductive success in Western American Crows (*Corvus brachyrhynchos hesperis*).

This is an unusual population of cooperative breeders (Caffrey 1992): breeding density was high, and core areas occupied by family groups were small, overlapped extensively with those of neighbors, and were not defended against conspecifics. A nonbreeding flock was resident on the study site. On average, 37% of breeding pairs had nonbreeding auxiliaries associating with them. Most auxiliaries (78%) were sexually immature yearlings. As yearlings, more females than males had delayed dispersal; most, but not all, of those at home (82%) served as helpers. More females than males assisted their parents in breeding; across all years of the study, 72% of helpers of known sex were female.

METHODS

I studied members of a resident population on the Balboa and Encino Golf Courses in Encino, California, from March 1985 through August 1990. I captured free-flying individuals using large walk-in traps and a cannon net. Trapped

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crows were weighed, measured, and marked with patagial tags and colored leg bands. The sex of marked individuals was determined either behaviorally or by use of a discriminant function based on morphological measurements (Caffrey 1992). Nestlings were weighed, measured, and marked between 32 and 38 days posthatching (mean nestling period = 41.0 ± 0.9 days, $n = 17$ nests; Caffrey 1992).

Breeding data were collected each spring. Pairs and associated auxiliaries were observed from nest-building until fledglings were at least 2 months old. Numbers of breeding attempts monitored in each year are given in Table 1.

BREEDING SUCCESS

I determined whether the nesting attempt produced any fledglings (nest success), the number of young fledged, the percent of fledged offspring that subsequently reached the ground safely (successful fledglings spent approximately 10 days in the canopy surrounding the nest tree before coming to the ground for the first time), the number of offspring alive 2 weeks postfledging, and the percent of those reaching the ground that were alive 2 months later. I used total number of young alive at 2 months, including zeros for failed nests, as a means of integrating all previous effects. I followed 97 marked nestlings from before fledging until the survivors were 2 months old. I also recorded the fates of 39 of those individuals up to 1 year of age.

I determined the timing of incubation and hatching by observing female behavior. For 1–3 days prior to the onset of incubation, females sat in or next to the nest and produced a characteristic “whine” vocalization (Lawton and Lawton 1985, Kilham 1986), the frequency of which increased up to the first day that the female sat on the nest continuously (day 1 of incubation). During incubation, females sat motionless for long periods, rising or leaving only to be fed by the male (or helper), stretch, defecate, or forage briefly. After 15–19 days, females began to shuffle around in the nest and intermittently put their heads down into it, with only their shaking tail-ends visible. I defined this as the day hatching began. I defined any young crow observed alive outside the nest as fledged. Fledging date was defined as the day nestlings left the nest permanently.

In all years, nests were observed at least every

3 days to determine their fate. When nests failed, I attempted to determine the cause; the ground below all failed nests was inspected. Additionally, in 1987 and 1988, 26% of failed nests were examined directly by climbing to them. I concluded that nests had failed due to predation either via direct evidence or in cases of sudden abandonment. On several occasions I saw potential predators attacking (Cooper’s and Red-shouldered Hawks, *Accipiter cooperii* and *Buteo lineatus*, respectively) or in (raccoon *Procyon lotor*, fox squirrel *Sciurus niger*) crow nests. Evidence that predators caused specific nest failures included: (a) finding nestling body parts, leg bands or patagial tags with raptor feathers, below raptor nests, or in Great Horned Owl (*Bubo virginianus*) pellets, and (b) the presence of predator feathers or fur, or structural damage, at failed nests. I concluded that nests suddenly abandoned had suffered predation because (1) all nests with direct evidence of predation were abandoned suddenly, whereas intact nests that failed for other known reasons (Results) were not, and (2) the distribution of nest failure dates (scaled to the start of incubation) was similar for nests known to have been predated and suddenly abandoned nests of uncertain fate.

The following variables (with the years in which they were examined indicated) were measured for each nest/pair in order to determine their relationship with reproductive success:

Helpers (1985–1990). Helpers were defined as nonbreeding auxiliaries that fed nestlings. There was little variation in the number of helpers among assisted pairs; in only 5 of 35 cases were there more than 1 (maximum = 2). Therefore, pairs were classified as either having help or not. Sample sizes were too small to examine any relationship between the presence of non-helping auxiliaries and nesting success.

Nest site characteristics. Nest and nest tree height (1985–1989) were estimated relative to a person of known height standing at the base of the tree. Relative height (1985–1989) was nest height divided by nest tree height. Nest tree types (1985–1989) included gymnosperms, eucalypts (*Eucalyptus* sp.), and sycamores (*Platanus* sp.). I also determined the number of trees in physical contact with each nest tree (1985–1989), on the chance that this might have been relevant for terrestrial predators. I scored nests subjectively for “concealment” (1985–1987): each nest received a score on a 5-point scale

based on its estimated degree of visibility from all sides.

Spatial characteristics. I classified core areas (the area of regular and heaviest use within an animal's home range) of pairs as interior or peripheral (1986–1989) based on nest locations within the study area (Caffrey 1992). Nest locations of crows and known avian predators were plotted on a map of the study site (1986–1989). I measured the distance from each nest to its nearest neighbor and all hawk and owl nests using a digitizer. I also determined, for those years, the number of other crow nests within 110 m (the farthest nearest neighbor distance measured) of each nest as an index of isolation.

In 1987 and 1988, I measured the availability of arthropods and annelids within eight different core areas each year from April through June. Each core area was sampled weekly, using pit-fall traps and the "surfacing-via-irritant" method (Tashiro 1987). Two pit-fall traps were dropped in each core area; I chose locations that were used heavily by foraging crows, but did not conflict with golf course restrictions. Each week I pooled the sampled arthropods from both pit-fall traps/core area. I used a 0.5-m² metal frame to enclose the area sampled using the surfacing-via-irritant method; the location for sampling each week was chosen randomly from maps of heavily foraged areas within core areas. Two and a half gallons of soapy water were poured into the metal frame over 10–15 min, and all arthropods and annelids surfacing within it were collected. In 1987, the dry weights of adult arthropods obtained were estimated from body lengths using the length-weight regression of Rogers et al. (1976). Dry weights of arthropod larvae and annelids were calculated from a regression equation generated from 12 sampled individuals ($W = 0.359L$, where W is weight in grams, and L is length in mm). In 1988, dry weights were obtained directly. Biomass of prey sampled by each method was analyzed for each core area per week.

Incubation date (1986–1990). The Julian date incubation began (defined above).

Nestling size. Nestling body mass and tarsus length were recorded (1985–1990) when nestlings were marked prior to fledging. Prefledging weight was found to correlate significantly with the number of days prefledging that nestlings were measured and marked ($r = -0.40$, $n = 39$,

TABLE 1. Percent of nesting attempts that succeeded in fledging young (n = number of attempts monitored). Attempts that failed before the status of associated auxiliaries could be determined are not included in "Assisted" or "Unassisted."

Year	Total	Assisted	Unassisted
1985	43 (7)	100 (2)	20 (5)
1986	44 (16)	71 (7)	28 (8)
1987	54 (26)	86 (7)	44 (18)
1988	38 (40)	30 (10)	40 (30)
1989	48 (25)	100 (6)	35 (17)
1990	33 (33)	100 (3)	27 (30)

$P < 0.05$). Therefore, I adjusted body mass to fledging date using the regression of body mass on days prefledging.

STATISTICAL ANALYSES

In examining breeding success, I first analyzed the correlates of nest success, and then excluded failed nests to analyze the sources of variation in subsequent stages. For most analyses, data were combined across years; I used log-linear models, ANCOVA, or two-way ANOVAs to determine that the relationships between specific factors and measures of breeding success were homogeneous among years. In only one case were years heterogeneous (1988: assisted nests were not more likely to fledge young than unassisted nests); I therefore dropped 1988 from the analysis of the effect of help on nesting success and repeated the test. To control for year effects on success for the 12 pairs with help in some years but not others, successful nesting attempts each year were given a score of 1 minus the mean percent nesting success for the population for that year (Table 1), and failures 0 minus the same value.

All P values throughout this paper represent two-tailed tests. Nonparametric tests were used when the assumptions of parametric tests were not met. Descriptive statistics are presented as mean \pm SE.

RESULTS

VARIATION IN BREEDING SUCCESS

Nest success. Only 63 (43%) of 147 nesting attempts monitored over 6 years fledged any young (Table 1). Some pairs renested when their nests failed early in the season, but no second attempt was ever successful ($n = 24$, 1985 through 1991).

TABLE 2. Mean \pm SE (n) Julian incubation dates. Across years, incubation began earlier at nests that succeeded (two-way ANOVA: $F_{1,105} = 6.5$, $P = 0.01$), and for pairs with assistance feeding nestlings (two-way ANOVA, effect of help: $F_{1,101} = 3.9$, $P = 0.05$).

Year	Succeed	Fail	Assisted	Unassisted
1986	89.3 \pm 1.1 (4)	84.0 \pm 2.1 (5)	88.0 \pm 2.0 (2)	86.2 \pm 2.2 (6)
1987	85.9 \pm 1.6 (13)	94.5 \pm 2.5 (12)	84.9 \pm 2.2 (7)	91.7 \pm 2.1 (17)
1988	89.3 \pm 1.6 (14)	90.9 \pm 1.4 (22)	86.2 \pm 1.5 (9)	91.6 \pm 1.2 (27)
1989	89.4 \pm 1.9 (10)	95.4 \pm 2.6 (11)	89.8 \pm 2.5 (6)	92.6 \pm 2.2 (13)
1990	89.1 \pm 1.1 (8)	96.3 \pm 1.9 (15)	89.0 \pm 4.0 (2)	94.3 \pm 1.5 (22)

Predation was the major cause of nest failure. Of 63 failures from 1985–1989, 52 (82.5%) were attributable to predation (direct evidence: 22; sudden abandonment: 30; observations in 1990 were insufficiently detailed for inclusion). My observations indicated Cooper's and Red-shouldered Hawks as the major predators of nestlings from 1985–1987. In the spring of 1988 a pair of Great Horned Owls nested at the north-eastern edge of the study area, and by 1989 they had become the major predators on crows of all ages. In 1990, the remains of at least seven different nestlings (two marked), two yearlings, and two adult crows (one a marked breeding female taken during incubation) were found in the area of the owl nest on eight different occasions during the breeding season. During this same period, I also found the remains of four different nestlings (three marked) in association with Great Horned Owl feathers on four separate occasions under an often used "killing tree." In addition, Great Horned Owl feathers and the patagial tags of two nestlings were found below one predated nest.

Of the 11 remaining nest failures (from 1985–1989), 5 (1 in 1985, 4 in 1988) blew down in high winds, the eggs never hatched at another (the female sat continuously for 4 weeks before the pair abandoned), and the decrease in feeding rates prior to abandonment at the other 5 suggested they, too, failed for intrinsic reasons.

Post-fledging success. Successful pairs of crows fledged an average of 1.93 ± 0.11 young ($n = 59$ successful nesting attempts). Of marked individuals that fledged ($n = 68$), 79.4% reached the ground safely (mean number to ground = 1.69 ± 0.12 , $n = 48$ successful attempts), and 88.9% of those survived to 2 months (mean number to 2 months = 1.5 ± 0.11 , $n = 42$ successful fledglings).

CORRELATES OF REPRODUCTIVE SUCCESS

Helpers. Assisted nests were more likely to fledge young in five of six years (Table 1). This between-year variation was significant when tested with a log-linear model (3-way interaction: $\chi^2_4 = 11.1$, $P < 0.03$). However, with the odd year (1988) omitted, the annual variation disappeared ($\chi^2_3 = 2.0$, $P = 0.57$) and nest success was strongly associated with helper presence ($\chi^2_1 = 38.8$, $P < 0.001$). Over all 6 years, 71.4% of 35 assisted nests fledged young vs. only 34.3% of 108 unassisted nests. I found no additional effects of helpers on number of young fledged, or on survival of fledglings to 2 weeks or 2 months. Helpers also did not affect the pre-fledging body mass or tarsus length of nestlings.

Other factors. Across years, successful pairs began incubation earlier in the season (Table 2). Because this was not the case in one year, the year vs. nest success interaction was marginally significant ($P = 0.053$). I found no additional effects of incubation date on number of young fledged, or their subsequent survival. Incubation date also was unrelated to the pre-fledging size of nestlings.

Some pairs were consistently more successful than others at producing surviving young. Among 21 pairs, each followed for 3–6 seasons, the number of young fledged (Kruskal-Wallis $H_{20} = 46.3$, $P < 0.001$) and the number alive 2 months later ($H = 35.9$, $P < 0.02$) varied significantly.

Heavier nestlings tended to experience higher fledging success than lighter ones (70% of 97 marked nestlings fledged), and larger nestlings (once fledged) tended to experience higher survivorship over the following 2-week period (Table 3). Considering all nestlings, the likelihood of fledging and surviving to age one appears to have been a function of pre-fledging size (Table 3).

TABLE 3. Relationships between pre fledging (PF) size (body mass and tarsus length) and subsequent survival to fledging, 2 weeks post fledging, and one year. Data include all nestlings in nests that went on to produce at least one fledgling. Mass standardized to fledging date. Data in rows are mean \pm SE (*n*). *P* values based on *t*-tests.

	Body mass			Tarsus length		
	Survived	Died	<i>P</i>	Survived	Died	<i>P</i>
PF-Fledge	319.6 \pm 6.1 (35)	275.1 \pm 11.0 (4)	0.02	54.79 \pm 0.47 (55)	53.22 \pm 0.69 (26)	0.07
Fledge-2 wks	325.4 \pm 6.7 (28)	291.6 \pm 12.0 (8)	0.03	55.37 \pm 0.48 (43)	52.84 \pm 1.0 (14)	0.04
PF-1 year	335.2 \pm 8.6 (17)	288.6 \pm 6.7 (15)	<0.001 ^a	56.09 \pm 0.50 (29)	53.01 \pm 0.55 (45)	<0.001 ^a

^a *P* < 0.05 by sequential Bonferroni method (Rice 1989).

I found no significant relationships between any measure of breeding success and any of the characteristics of nests or core areas. The results from both invertebrate prey sampling methods in 1987 and 1988 demonstrated no differences between core areas in biomass of prey available to foraging crows (Friedman two-way ANOVAs). Nest success in sampled core areas was low in both years (1987: 37%; 1988: 25%), and small sample sizes prohibited analysis of any direct relationship between prey availability and reproductive success. Finally, I found no relationship between a nest's success and its proximity to the nearest raptor nest or the success of other nearby crow nests.

RELATIONSHIPS BETWEEN HELPING, INCUBATION DATE, AND PAIR DIFFERENCES

In most years, assisted pairs began incubation earlier than unassisted ones (Table 2). When incubation dates were scaled to the median incubation date within each year and then combined across years, mean incubation date for assisted pairs was approximately 4 days earlier than that for unassisted pairs ($t_{60} = 3.5$, $P < 0.001$). Because some pairs were represented more than once in this analysis, a possible explanation for this relationship was that different pairs consistently started early or late in successive years and that early incubators, being more successful, were more likely to have helpers in the following year. In support of this, incubation dates of pairs were positively related across successive years ($r = 0.48$, $n = 27$, $P < 0.05$; incubation dates were standardized to the annual median date for this analysis). However, multiple regression demonstrated significant partial effects of both helper presence ($t = 2.19$, $P = 0.03$) and incubation date ($t = 2.66$, $P < 0.01$) on nest success. Thus helping and nest success were re-

lated even after taking into account differences in incubation date.

Differences in pair success also were correlated with helping. The proportion of years in which a pair had help was positively related to the proportion of years in which any young fledged ($r_s = 0.44$, $P < 0.05$) and the mean number of young surviving to 2 months ($r_s = 0.47$, $P < 0.05$). This indicated that either some pairs had help because they were consistently successful, or that they were successful because they consistently had help.

To tease apart these possibilities, I examined data for 12 pairs that had help in some years (of the six [$n = 2$ pairs], five [$n = 3$], four [$n = 5$], or three [$n = 2$] years they were monitored) but not in others. The nest success of these pairs in years when they had help was positively correlated with success in years without help ($r = 0.70$, $P = 0.01$). Thus, some pairs were consistently successful regardless of whether or not they had help. In addition, these pairs were not significantly more successful at fledging young in years when they were assisted (controlling for year effects, Wilcoxon $W = -4$, $P = 0.26$). Helpers may have conferred a small benefit upon breeders, because median nest success scores across years were three times higher for these pairs when assisted, yet this "effect" may have been a function of consistently successful pairs succeeding, with helpers present, in years when most other pairs failed to fledge young. When successful, the number of fledglings produced by these pairs when assisted ($\bar{x} \pm SE = 2.07 \pm 0.23$, $n = 15$ successful attempts) did not differ from the number fledged when unassisted (1.88 ± 0.29 , $n = 16$ successful attempts: Mann-Whitney $U = 235$, $P = 0.39$; only pairs with successes under both conditions considered). In

addition, for five pairs I was able to examine the relationship between having help or not and success, given that potential helpers had been produced the year before; for pairs that were successful in year x , their success in year $x + 1$ did not appear to be a function of whether or not their yearlings remained home and helped (controlling for year effects, Wilcoxon $W = -9$, $P = 0.31$; mean nest success scores were higher for three of five when assisted, and for two of five when unassisted). The data thus suggest that an effect of help on nesting success, if any, was weak once differences between pairs had been controlled for.

DISCUSSION

These data demonstrate striking differences in the breeding success of pairs both within seasons and over several years. Much of this reflects success in fledging any young in the face of high levels of predation on nestlings, although the subsequent survival of fledglings also was a factor. Despite finding that assisted pairs initiated incubation earlier and were significantly more successful at fledging young than unassisted pairs, and that pairs that were helped more often were more consistently successful, these relationships between the presence of helpers and nesting success were misleading. Upon closer inspection, it appears that for Western American Crows, success breeds helping rather than vice versa.

Despite the fact that pairs with help were more successful than unassisted pairs at fledging young, helpers were not an important cause of this effect. When I compared a pair's success in years with and without help, there was no significant increase in breeding success in assisted years. Comparing data in this way, however, introduces a bias toward finding no effect of help for species in which helpers are primarily yearlings (J. Dickinson, pers. comm.): for pairs that make the transition between the conditions of having help and not, pairs with a helper in year x were, on average, more successful in year $x - 1$ (when unassisted) than random groups; conversely, pairs unassisted in year x were, on average, less successful in year $x - 1$ (when assisted) than random groups. Thus, restricting the analysis to such pairs statistically biases against an effect of helpers. Yet, several aspects of the data for my population mitigate against this bias. First is the strong correlation within pairs for

nest fate among years, whether pairs were assisted or not. Second, it was not uncommon for unassisted attempts to have been preceded by successful years. Although the majority of helpers in the population were yearlings, 25% were not (Caffrey 1992); five individuals remained with their parents for more than 1 year (up to 3 additional years), and in all cases, helped in some years but not in others. In addition, 25% of yearlings were not at home, and 18% of those at home did not help (Caffrey 1992). As such, for 5 of the 12 pairs that had help in some years but not others, 9 of 19 successful years (29% of all the successes for these 12 pairs) were followed by years without assistance. Additionally, in one case, an unsuccessful year was followed by a year with help—a widowed breeder joined and assisted one of her neighboring pairs. Thirdly, pairs with yearlings alive were not more successful at fledging young when assisted by those yearlings than they were when their yearlings chose not to help. Thus it appears that, for this population, some pairs are consistently more successful than others, and that those pairs more often have help because prior offspring often act as helpers in their first (or more rarely, second) year (Caffrey 1992). The apparent slight increase in the likelihood of fledging young when assisted may have been an artifact of these superior pairs succeeding, fortuitously with help, in otherwise poor years (thus their adjusted nest success scores for those years were comparatively high). This suggests that helpers may not be increasing their indirect fitness by helping. It also raises the question of why some pairs are more successful than others.

One contributing factor appears to be differences in nesting date. Different pairs nested consistently early or late in successive years, and early nests suffered lower levels of predation. Later in the season, when predation pressure intensified, the nestlings from some early nests had already fledged, or were old enough to jump to safety when predators attacked. I recorded five cases where one or more brood members were taken by a raptor but a sibling survived by jumping out of the nest. Laying date is thought to be determined by the female's ability to obtain the food necessary for egg production (Perrens 1970), and presumably "better" females accomplish this earlier (Price et al. 1988). Although incubation date contributed to differences in breeding success among pairs, other factors

must also have been important; mean annual success and mean incubation date were at best weakly related (number fledged: $r_s = -0.39$, $n = 21$ pairs over 3–5 years, $0.05 < P < 0.1$; number alive at two months: $r_s = -0.35$, $n = 21$, $0.1 < P < 0.2$).

Age of breeders and/or breeder experience can affect reproductive outcome (Walters 1990, Russell and Rowley 1993, Komdeur 1996a, 1996b), and older and/or more experienced females often begin laying earlier (Roskaft et al. 1983, Reese and Kadlec 1985, Nol and Smith 1987). Unfortunately, the exact ages and experience histories for many breeders in my population were unknown. However, the importance of these variables by themselves is questionable, because many breeders known to be at least 5 years old at marking (based on mouth color patterns) subsequently failed year after year.

Territory quality was not a confounding variable because crows in this population were not territorial: breeders did not engage in any type of area defense, and individuals easily moved among areas on and off the study site (Caffrey 1992). Given the high levels of nest predation, I anticipated that other factors, particularly nest placement, would influence success, but the data did not support this idea. Because of the whining and begging of incubating and brooding females, frequent feeding trips by parents and helpers, and the begging of older nestlings, even a concealed nest may be easy for diurnal predators to locate, especially given the long nestling period. The high density of breeders, auxiliaries, and nonbreeding flock members in this population (Caffrey 1992) may explain why family group size did not affect the likelihood of diurnal nest predation; everybody mobbed detected predators. For nocturnal predation, it is difficult to imagine any mechanism by which family members might thwart its occurrence. Nest "concealment" may have been an important consideration with regard to predation by Great Horned Owls, but I discontinued estimating this variable after 1987, prior to the arrival of the owls, because of concern over its subjectiveness.

Prefledging size was the only factor found to influence postfledging survivorship. The tendency for larger nestlings to be more likely to fledge and survive the 2-week postfledging period, and their higher survivorship to one year was not surprising. Similar results have been found for

other passerines (Fiala 1981, Roskaft 1983, Mumme 1992).

In conclusion, helpers in this population did not appear to be increasing the production of nondescendent kin by way of increasing the success of individual nesting attempts. The feeding contributions made by helpers varied among years, and feeding rates were not related to any measure of breeding success (Caffrey 1999). Although assisted females contributed significantly less to feeding nestlings than unassisted ones, the lightened workload of assisted females did not translate into increased subsequent survival or an increase in the success of renesting attempts (Caffrey 1999). Thus, helpers did not appear to be benefiting indirectly through their participation in the breeding activities of their parents. They did not appear to be benefiting directly, either, in ways postulated for other species (Koenig and Mumme 1990, Emlen 1991, Cockburn 1998). For 2 and 3-year-olds whose fates were known, survivorship did not differ for individuals that did vs. did not delay dispersal, or did vs. did not help (Caffrey 1992). Nor was helping a stepping stone to breeding status; quality breeding habitat was not limited, and helping was not a means of inheriting a mate or producing future allies or helpers (Caffrey 1992). Because females helped more often than males (Caffrey 1992) and females have a greater role in nest building and early brood care (pers. observ.), it is possible that helping may serve to provide an opportunity for learning breeding skills. Any learning-related benefits were not manifested early in the breeding histories of individuals, however, as the first breeding attempts of all individuals, regardless of sex, age, or past experience, were unsuccessful ($n = 26$).

Is helping behavior in this population currently nonadaptive? Is breeding on an urban golf course (with an abundance of food and nearby suitable nest trees) so totally removed from the historical conditions under which helping may have been adaptive as to render its evolutionary significance moot? To wit, crows in this population were highly unusual in their complete lack of resource defense (Caffrey 1992), and known sources of mortality for breeding females were importantly "unnatural" as well as natural: cars and golf balls killed almost as many as Great Horned Owls (Caffrey 1999). That 9 of 52 auxiliaries at home for the breeding season did not help at the nest (Caffrey 1992) suggests that

helping is not simply the inevitable consequence of strong selection for feeding begging nestlings combined with delayed dispersal (Jamieson 1991). Might the tendency for offspring to delay dispersal and help merely reflect phylogenetic inertia (Cockburn 1996)? Is non-helping in individuals delaying dispersal currently being favored? Is helping behavior being maintained via gene flow from surrounding populations occurring in habitats where territoriality exists (per. observ.) and selection pressures may differ? Are sexually mature female helpers sneaking eggs into the nests they attend? Regrettably, these provocative questions are unlikely to ever be answered for this population.

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