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Feeding Rates and Individual Contributions to Feeding at Nests in Cooperatively Breeding Western American Crows

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Helpers increase the reproductive success of breeders in many species of cooperatively breeding birds. Several mechanisms by which they do so involve the feeding of nestlings. The presence of additional feeders may result in increased amounts of food brought to nests, which can increase growth rates of nestlings (Dickinson et al. 1996) and reduce starvation (Rowley 1978, Reyer 1980, Emlen and Wrege 1991, Heinsohn 1992). Alternatively, helpers may not increase total feeding rates at nests but instead reduce the workload of one or both breeders. Lightening the load of breeders may translate into increased success in several ways. Relief of feeding responsibilities may allow breeders to devote more time to vigilance and antipredator behavior (Rabenold 1984, Austad and Rabenold 1985). For some species, subsequent survival is higher for members of assisted pairs than for unassisted ones (Stallcup and Woofenden 1978, Reyer 1984, Russell and Rowley 1988). Additionally, in some multiple-brooded species, helper assistance results in shortened interbrood intervals, allowing for the production of more clutches per season (Rowley 1965, Brown and Brown 1981, Rabenold 1984, Russell and Rowley 1988).

Here, I describe the feeding contributions made by individuals at assisted and unassisted nests of Western American Crows (*Corvus brachyrhynchos hesperis*) and examine the effects that the feeding contributions of helpers have on nestling feeding rates. I also examine other factors that could affect feeding rates, and the consequences of variation in feeding rates on breeding success.

Methods.—I studied members of a resident population of crows on the Balboa and Encino golf courses in Encino, California, from March 1985 through August 1990. The habitat consisted of tracts of grass separated by rows of trees, with additional clumps of trees scattered throughout the site. The climate was southern Californian Mediterranean, with hot, dry summers and occasional winter rains between December and February.

I captured 173 free-flying individuals (63 males, 54 females, 56 unsexed) using large walk-in traps and a cannon net. Trapped crows were weighed, measured, and marked with identical patagial tags bear-

ing two letters, a numbered metal leg band, and a unique combination of colored plastic leg bands. The sex of marked individuals was determined either behaviorally or by using a discriminant function based on morphological measurements (Caffrey 1992). Nestlings ($n = 97$) were also weighed, measured, and marked between 32 and 38 days posthatching (mean nestling period = $41.0 \pm \text{SE of } 0.9$ days; Caffrey 1992).

I determined the timing of incubation and hatching by observing female behavior. For one to three 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 were motionless for long periods, rising or leaving only to be fed by the male (or helper), stretch, defecate, or forage. After 15 to 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. All brood members left the nest on the same day at 88% of nests where fledging date was determined ($n = 17$).

I studied feeding rates at 19 nests (9 assisted and 10 unassisted) during the breeding seasons of 1986 through 1988; nests were chosen on the basis of visibility (mean nest height = 18.89 ± 0.33 m, $n = 88$) and the number of marked individuals present. Each nest was observed three to five times per week. Observation periods for each nest were rotated to ensure coverage at all times of the day within different weeks of the nestling period. The day hatching began was set as day 0. For days 0, 1, and 2, nests were observed for 30 to 120 min ($\bar{x} = 74.1 \pm 7.2$ min, $n = 41$ periods). From day 3 onward, nests were observed for periods of 60 to 180 min ($\bar{x} = 112.9 \pm 2.5$ min, $n = 431$ periods). Observations continued until nests failed or young fledged. Approximately two-thirds of all observations were made from a car, using a 20 \times spotting scope; the remainder were recorded with a distantly placed video camera and reviewed later.

I defined a feeding trip as any instance in which a

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bird arrived with food and the nestlings were fed, either directly or via the brooding female. For birds that carry food in filled crops, rather than as individual items in their bills, variance in the volume of food per trip has been suggested to be low, on the basis that filling a crop completely would be most efficient (Buitron 1988). Thus, feeding trips appear to be a reasonable comparative measure regarding the amount of food being brought to nests. For all marked birds, or in cases where only one bird was unmarked, feeding trips were attributed to individuals. For each observation period, total and individual trips per time observed were determined. For individuals, mean rates and the percentage of total trips made were compared over the entire nestling period.

Annual survivorship, from the beginning of one breeding season to the next, was calculated as the percentage of marked breeders in year x that was alive in year $x + 1$. Means and standard errors were then calculated across the seven years of observations for each sex. Annual survival rates were reasonably unbiased because the large size of these birds, coupled with their tenacity to the study site and surrounding areas during the entire year and my presence at least once per week in all years, yielded annual resighting/recapture rates of 100%; all individuals included in the survivorship analyses were seen at least once every month until they died or disappeared permanently. Several breeders that were assisted in one or more years were unassisted in others; thus, to test for an effect of helpers on subsequent survivorship, I analyzed differences in survival over the year following a given nesting attempt for assisted and unassisted breeders, treating years independently. Sample sizes for these analyses were considerably smaller than those for overall survivorship analysis, in part because of the number of nesting failures that occurred before helper status could be confirmed.

All P -values are from two-tailed tests unless indicated otherwise. Nonparametric tests were used when the assumptions of parametric tests were not met. Descriptive statistics are presented as $\bar{x} \pm 1$ SE.

Results.—Over all years, the main effect of helpers was not significant ($F = 1.06$, $df = 1$ and 327 , $P = 0.304$), but significant interactions existed between year and helping, and year and all potential covariates (days posthatching and its square, and date of observation and its square). Thus, data for different years were analyzed separately. Within years, observation date and its square had no significant main effects or interactions, so these variables were dropped from further analyses. Helper effects on feeding rates were examined with analysis of covariance (ANCOVA), with days posthatching and its square as covariates. Both covariates were highly significant for all years ($P < 0.0001$ in all cases). Feeding rates differed significantly at assisted and unassisted nests

in all years (1986, $F = 4.18$, $df = 1$ and 104 , $P = 0.043$; 1987, $F = 4.25$, $df = 1$ and 115 , $P = 0.042$; 1988, $F = 7.89$, $df = 1$ and 118 , $P = 0.006$), but the direction of the difference was not consistent across years (Fig. 1).

Analysis of variance in feeding rates demonstrated a significant interaction between year and nest fate (succeed or fail); thus, data for different years were analyzed separately. Within years, ANCOVA (with days posthatching and its square, and observation date and its square as covariates) demonstrated significant differences in feeding rates at nests that succeeded or failed (1986, $F = 4.09$, $df = 1$ and 98 , $P = 0.046$; 1987, $F = 5.67$, $df = 1$ and 109 , $P = 0.019$; 1988, $F = 16.61$, $df = 1$ and 112 , $P < 0.0001$); regression coefficients demonstrated that the relationship differed among years here, too (1986 and 1987, feeding rates higher at nests that succeeded; 1988, feeding rates higher at nests that failed).

For individual nests over all years, feeding rates (residuals from best-fit second-order polynomial for all successful nests) adjusted for days posthatching were not related to any other measure of nesting success. Feeding rates were unrelated to (1) brood size at marking ($r = 0.174$, $n = 8$), (2) brood size at fledging ($r = 0.199$, $n = 8$), (3) total brood mass at marking ($r = 0.106$, $n = 5$), (4) mean nestling mass at marking ($r = -0.573$, $n = 5$), (5) mean nestling tarsus length at marking ($r = -0.099$, $n = 7$), and (6) length of the nestling period ($r = 0.183$, $n = 8$).

Unassisted females fed nestlings at significantly higher rates than did assisted females and made a greater proportion of total feeding trips than did females with help (Table 1). The difference in percent total trips between unassisted and assisted females was approximately 31%, and helpers made about 36% of all feeding trips (Table 1). Over all nests, males contributed significantly more to feeding nestlings than did females (paired $t = 2.90$, $df = 5$, $P = 0.034$). Mean feeding rates for unassisted and assisted males were almost identical, although the proportion of total feeding trips was lower for males with help (Table 1).

Sample sizes were too small to measure the direct effects of reduced female feeding rates on survival or on renesting intervals after a failed first attempt. However, to assess the possible effects of this reduction, I compared female survivorship and renesting intervals for all assisted and unassisted pairs for which I had data. Over seven years (1985 to 1992), mean annual survivorship for marked female breeders was $94.3 \pm 0.03\%$; of 23 individuals observed over 67 crow-years, five died and two disappeared. Known causes of death included predation by Great Horned Owls (*Bubo virginianus*) during the incubation period (two unassisted females and one with two potential helpers), being hit by a golf ball (an assisted female during the nestling period), and being hit by a car (one female with nest built but before in-

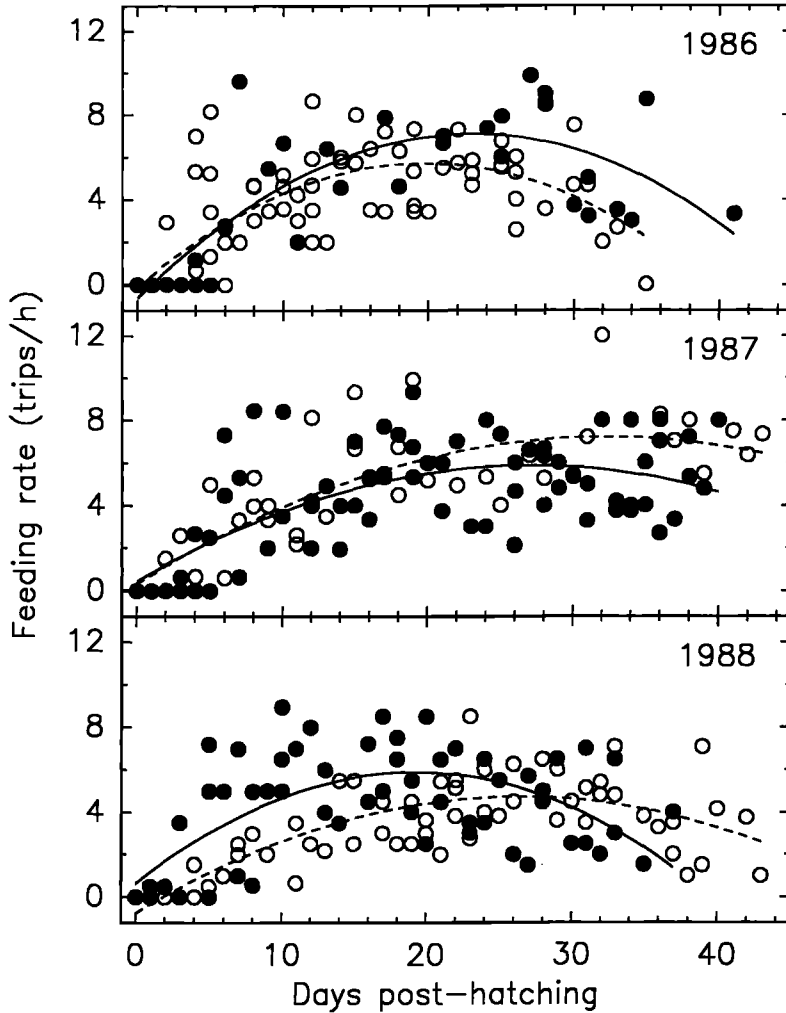


FIG. 1. Best-fit second-order polynomial for assisted (solid circles and lines) versus unassisted (open circles, dashed lines) American Crow nests.

cubation began; she had been assisted in her previous nesting attempt). One of the two disappearances occurred at the same time the female's nestlings were taken by a Great Horned Owl. Six of these seven losses (86%), or four of the five "natural" losses (80%), occurred during the breeding season, and five of the seven occurred in the single year 1991–92. Females assisted by helpers during the breeding season did not experience increased survivorship during the subsequent year (0 deaths/8 assisted females, 1 death/38 unassisted females; $\chi^2 = 0.21$, $P > 0.50$). For marked male breeders over the same seven years, mean annual survivorship was $95.1 \pm 0.02\%$; of 27 individuals observed over 105 crow-years, four died and one disappeared. Only one of those losses (20%) occurred during the breeding season (an unassisted

male found during the nestling stage with no evidence as to cause of death). Having assistance during the previous breeding season did not increase the likelihood of surviving to the next breeding season for males, either (2 deaths/24 assisted males, 1 death/55 unassisted males; $\chi^2 = 1.76$, $P > 0.10$). The presence of helpers did not appear to reduce re-nesting intervals after nest failure, although sample sizes were small (assisted, $\bar{x} = 9.0 \pm 2$ days, $n = 2$; unassisted, $\bar{x} = 10.0 \pm 0.6$ days, $n = 10$).

Discussion.—Despite small samples, I found evidence that breeding females reduced their nestling feeding contributions when assisted by helpers. Beyond that, no consistent relationships occurred between helpers, feeding rates, and any measure of nesting success, other than the fact that feeding rates

TABLE 1. Feeding rates at assisted versus unassisted American Crow nests. Values are $\bar{x} \pm SE$, with n in parentheses. P -values are from one-tailed Mann-Whitney U -tests.

	Assisted	Unassisted	P
Trips per hour			
Total	4.6 \pm 0.36 (9)	3.8 \pm 0.32 (10)	0.07
Males	2.0 \pm 0.28 (4)	2.0 \pm 0.44 (3)	0.43
Females	0.6 \pm 0.23 (3)	1.4 \pm 0.27 (3)	0.05
Helpers	1.6 \pm 0.27 (5)	—	—
Proportion of total feeding trips			
Males	42.8 \pm 0.02 (4)	55.0 \pm 0.06 (3)	0.06
Females	13.7 \pm 0.03 (3)	45.0 \pm 0.06 (3)	0.05
Helpers	35.7 \pm 0.05 (5)	—	—

were unrelated to several fitness-related measures. Not only did any effect of help on nestling feeding rates vary among years, the "effect" was such that assisted nests had lower feeding rates than unassisted ones in one of the three years. This was surprising given that females do very little feeding of nestlings for the first two weeks, during which time they brood almost continuously (pers. obs.). That notwithstanding, the evolutionary significance of the variable nature of helper effects on feeding rates is to some extent moot, because variance in feeding rates apparently did not contribute to variance in breeding success. The most pressing constraint on reproductive success in this population was predation (only 43% of 147 attempts monitored over six years fledged any young; Caffrey 2000); variance in the number of young fledged from successful nests was low ($\bar{x} = 1.93 \pm 0.11$; Caffrey 2000). Of the 19 nests observed in the present study, 8 were lost to predation (and another blew down during high winds). Thus, other than lightening the load of breeding females, helper feeding efforts did not contribute to breeding success.

A reduction in feeding workload of breeders in the presence of helpers has been documented for many species of cooperative breeders (Lewis 1981, Raitt et al. 1984, Curry 1988). In some cases, both breeders decrease individual feeding rates (Brown et al. 1978, Gibbons 1987, Dickinson et al. 1996); in others, it is primarily males (Rabenold 1984, Sherley 1990, Dickinson et al. 1966) or females (Rowley 1981, Austad and Rabenold 1985, Crick and Fry 1986, Tideman 1986). It seems reasonable that females would have more to gain by exploiting helper contributions. Female passerines commit substantial amounts of energy to egg laying (Perrins 1970) and may benefit in both the short and long term by capitalizing on the chance to recoup lost energy reserves. In some species, females experience higher mortality than males during the breeding season as a result of their weakened state or predation during incubation or brooding (Coulson 1960, Koenig and Mumme 1987, Mar-

zluff and Balda 1990, this study). In others, a decrease in individual feeding rates is associated with an increase in subsequent survival (Lewis 1982, Woolfenden and Fitzpatrick 1984, Rabenold 1990). Such helper-mediated survivorship benefits, however, do not appear to accrue to female crows in my study population.

All three females known to have died natural deaths were incubating when taken by Great Horned Owls; it is difficult to imagine a mechanism by which having an auxiliary present during the day might influence the outcome of such an event (only breeding females incubate, and helpers roosted off the study site). The same is true for the female presumably taken by a Great Horned Owl at the same time as her nestlings. And, although female crows invest energy in egg laying and forego much of their own maintenance behavior to incubate eggs and brood young nestlings (pers. obs.), they do not appear to be excessively stressed later in the season. Females without assistance from helpers fed nestlings at rates twice those of assisted females. Additionally, the female from an unassisted nest in which the male was found dead 26 days after the eggs hatched not only continued to feed nestlings on her own for 10 days, she doubled her rate of the preceding week (to 2.8 ± 0.32 trips per h). Mean annual survivorship over seven years for breeding females was 94%, and assisted females were no more likely to survive the subsequent year than were unassisted ones. Clearly, female crows were not working at maximum capacity, nor were they dying as a consequence of reproductive effort.

One reproductive benefit of lightening breeder workload, particularly that of females, is the production of more clutches per season via shorter intervals between nesting attempts. For Splendid Fairy-Wrens (*Malurus splendens*; Russell and Rowley 1988) and Gray-crowned Babblers (*Pomatostomus temporalis*; Brown et al. 1978), this benefit was the direct result of males and helpers taking over care of fledglings, permitting females to initiate a second clutch. Western American Crows are not multiple brooded. However, because nest-failure rate in this population was high (Caffrey 2000), I considered the possibility that a reduction in the workload of females would allow them to renest sooner after a failed first attempt. The sample size was small for assisted pairs where both failure date and renesting incubation date were known, but because no second attempt was successful ($n = 24$, 1985 through 1991), shortened renesting intervals are unlikely to be an important consideration.

A final possibility is that a lightened feeding load allowed breeding females to be more vigilant (Rabenold 1984, Austad and Rabenold 1985). Once females stopped brooding and began feeding nestlings, they generally spent more time than males at or near nests (pers. obs.). However, although loss of

ests to predators was the major cause of breeding failure in this population, and assisted pairs had a significantly greater chance of fledging young than unassisted pairs, I found no evidence that helpers caused this effect (Caffrey 2000). Thus, I found no compelling evidence that a lightened feeding load allowed breeding females to guard their nestlings more effectively.

Feeding rates have been shown to influence annual reproductive success in some species of cooperative breeders. In the presence of helpers, increased feeding rates reduced starvation and resulted in more fledglings per nest (Dyer 1983, Curry and Grant 1990, Heinsohn 1995) and also increased the subsequent survivorship of nestlings that fledged (Emlen and Wrege 1991). In Florida Scrub-Jays (*Aphelocoma coerulescens*), higher feeding rates at assisted nests resulted in more rapid growth and development of the young, contributing to the larger size of nestlings and their subsequent higher survival (Mumme 1992). Yet, feeding rates at crow nests were not related to any measure of breeding success. There was no consistent difference in feeding rates at nests that either succeeded or failed, and feeding rate was not related to brood size at fledging or to the pre-fledging size of nestlings (which affects their subsequent survival; Caffrey 2000). A shortened nestling period might make nests less vulnerable to predation (Strahl and Schmitz 1990), but no relationship existed between feeding rate and the number of days nestling crows spent in the nest. Given the above, along with the variable nature of helper effects on feeding rates and the lack of any survivorship or nesting benefits to load-lightened females, these data demonstrate that the feeding contributions of helpers did not contribute to variance in breeding success in Western American Crows.

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LITERATURE CITED

- AUSTAD, S. N., AND K. N. RABENOLD. 1985. Reproductive enhancement by helpers and an experimental examination of its mechanism in the Bicolored Wren: A facultatively communal breeder. *Behavioral Ecology and Sociobiology* 17:19–27.
- BROWN, J. L., AND E. R. BROWN. 1981. Kin selection and individual selection in babblers. Pages 244–256 in *Natural selection and social behavior: Recent research and new theory* (R. D. Alexander and D.W. Tinkle, Eds.). Chiron Press, New York.
- BROWN, J. L., D. D. DOW, E. R. BROWN, AND S. D. BROWN. 1978. Effects of helpers on feeding of nestlings in the Grey-crowned Babbler (*Pomatosotomus temporalis*). *Behavioral Ecology and Sociobiology* 4:43–59.
- BUITRON, D. 1988. Female and male specialization in parental care and its consequences in Black-billed Magpies. *Condor* 90:29–39.
- CAFFREY, C. 1992. Female-biased delayed dispersal and helping in American Crows. *Auk* 109:609–619.
- CAFFREY, C. 2000. Correlates of reproductive success in cooperatively breeding Western American Crows: Helpers don't really help. *Auk* 117: in press.
- COULSON, J. C. 1960. A study of mortality in the starling based on ringing records. *Journal of Animal Ecology* 29:251–71.
- CRICK, H. Q. P., AND C. H. FRY. 1986. Effects of helpers on parental condition in Red-throated Bee-eaters (*Merops bullocki*). *Journal of Animal Ecology* 55:893–906.
- CURRY, R. L. 1988. Influence of kinship on helping behavior in Galapagos Mockingbirds. *Behavioral Ecology and Sociobiology* 22:141–152.
- CURRY, R. L., AND P. R. GRANT. 1990. Galapagos Mockingbirds: Territorial cooperative breeding in a climatically variable environment. Pages 289–332 in *Cooperative breeding in birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- DICKINSON, J. L., W. D. KOENIG, AND F. A. PITELKA. 1996. Fitness consequences of helping behavior in the Western Bluebird. *Behavioral Ecology* 2: 168–177.
- DYER, M. 1983. Effect of nest helpers on growth of Red-throated Bee-eaters. *Ostrich* 54:43–46.
- EMLEN, S. T., AND P. H. WREGE. 1991. Breeding biology of White-fronted Bee-eaters at Nakuru: The influence of helpers on breeder fitness. *Journal of Animal Ecology* 60:309–326.
- GIBBONS, D. W. 1987. Juvenile helping in the Moorhen. *Animal Behaviour* 35:170–181.

- HEINSOHN, R. G. 1992. Cooperative enhancement of reproductive success in White-winged Choughs. *Evolutionary Ecology* 6:97-114.
- HEINSOHN, R. G. 1995. Hatching asynchrony and brood reduction in cooperatively breeding White-winged Choughs. *Emu* 95:252-258.
- KILHAM, L. 1986. Vocalizations by female American Crows early in the nesting period. *Journal of Field Ornithology* 57:309-310.
- KOENIG, W. D., AND R. L. MUMME. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton University Press, Princeton New Jersey.
- LAWTON, M. F., AND R. O. LAWTON. 1985. The breeding biology of the Brown Jay in Monteverde, Costa Rica. *Condor* 87:192-204.
- LEWIS, D. M. 1981. Determinants of reproductive success of the White-browed Sparrow Weaver, *Plocepasser mahali*. *Behavioral Ecology and Sociobiology* 9:83-93.
- LEWIS, D. M. 1982. Cooperative breeding in a population of White-browed Sparrow Weavers *Plocepasser mahali*. *Ibis* 124:511-522.
- MARZLUFF, J. M., AND R. B. BALDA. 1990. Pinyon Jays: Making the best of a bad situation by helping. Pages 197-238 in *Cooperative breeding in birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- MUMME, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida Scrub Jay. *Behavioral Ecology and Sociobiology* 31:319-328.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242-255.
- RABENOLD, K. N. 1984. Cooperative enhancement of reproductive success in tropical wren societies. *Ecology* 65:871-85.
- RABENOLD, K. N. 1990. *Campylorhynchus* wrens: The ecology of delayed dispersal and cooperation in the Venezuelan savanna. Pages 157-196 in *Cooperative breeding in birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- RAITT, R. J., S. R. WINTERSTEIN, AND J. W. HARDY. 1984. Structure and dynamics of communal groups in the Beechey Jay. *Wilson Bulletin* 96:206-227.
- REYER, H.-U. 1980. Flexible helper structure as an ecological adaptation in the Pied Kingfisher (*Ceryle rudis rudis* L.). *Behavioral Ecology and Sociobiology* 6:219-227.
- REYER, H.-U. 1984. Investment and relatedness: A cost/benefit analysis of breeding and helping in the Pied Kingfisher (*Ceryle rudis*). *Animal Behaviour* 32:1163-78.
- ROWLEY, I. 1965. The life history of the Superb Blue Wren *Malurus cyaneus*. *Emu* 64:251-97.
- ROWLEY, I. 1978. Communal activities among White-winged Choughs, *Concorax melanorhamphos*. *Ibis* 12:178-97.
- ROWLEY, I. 1981. The communal way of life in the Splendid Wren, *Malurus splendens*. *Zeitschrift für Tierpsychologie* 55:228-67.
- RUSSELL, E., AND I. ROWLEY. 1988. Helper contributions to reproductive success in the Splendid Fairy-Wren (*Malurus splendens*). *Behavioral Ecology and Sociobiology* 22:131-140.
- SHERLEY, G. H. 1990. Co-operative breeding in Rifleman (*Acanthisitta chloris*). Benefits to parents, offspring, and helpers. *Behaviour* 112:1-22.
- STALLCUP, J. A., AND G. E. WOOLFENDEN. 1978. Family status and contribution to breeding by Florida Scrub Jays. *Animal Behaviour* 26:1144-56.
- STRAHL, S. D., AND A. SCHMITZ. 1990. Hoatzins: Co-operative breeding in a folivorous Neotropical bird. Pages 131-156 in *Cooperative breeding in birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- TIDEMAN, S. C. 1986. Breeding in three species of fairy-wrens (*Malurus*): Do helpers really help? *Emu* 86:131-138.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: Demography of a cooperatively breeding bird. Princeton University Press, Princeton, New Jersey.

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