

EVIDENCE FOR OBLIGATE MALE PARENTAL CARE IN BLACK-BILLED MAGPIES

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ABSTRACT.—The hypothesis that an absolute need for male parental care maintains monogamy in bird populations has been rejected in almost all studies where males have been removed. However, most of these studies examined species in which males contributed less parental care than females. In Black-billed Magpies (*Pica pica*), the sexes have relatively similar levels of parental care. We removed male magpies during the laying period to early in the nestling period and found that 100% of unaided females failed to produce any offspring ($n = 20$), while 48% of females with mates ($n = 106$) failed to produce any young. The nest-visit rate of unaided females was lower than that for both the male and female at control nests during the incubation and nestling periods. Unaided females made <50% of the visits of control pairs after hatch, when many (54%) nests of unaided females failed. Male parental care is more important in Black-billed Magpies than in any other passerine in which the need for male parental care has been examined experimentally. This does not necessarily indicate that an absolute need for male parental care maintains monogamy in magpies. It may still be possible for males to produce more offspring by aiding two females, if two females can each produce some offspring with a fraction of the male's total parental care. We argue that this is unlikely because male magpies do not appear to assist more than one mate successfully. We believe that a need for male parental care is the most likely factor maintaining monogamy in this population of Black-billed Magpies. Received 25 November 1989, accepted 8 May 1989.

Most species of birds are monogamous, in contrast to the widespread occurrence of polygyny in other vertebrates (Lack 1968, Møller 1986). Because males contribute more parental care in monogamous than polygynous birds (Verner and Willson 1969, Møller 1986), monogamy has often been explained by a need for male parental care in order to produce offspring successfully (Lack 1968, Emlen and Oring 1977, hypothesis 1 of Wittenberger and Tilson 1980). However, this association does not necessarily indicate what factors maintain monogamy in bird populations. Male parental care would only explain monogamy in a population when females cannot rear any offspring without male parental care (hypothesis 1 of Wittenberger and Tilson 1980) or when the reduced amount of male parental care often associated with secondary mate status (e.g. Lifjeld et al. 1987) makes pairing with bachelor males more profitable to females than pairing with already-mated males (hypothesis 2 of Wittenberger and Tilson 1980). Experimental removal of males can indicate the importance of male parental care to female reproductive success and, thereby, its significance in the maintenance of monogamy.

Almost all male-removal studies have found that unaided or "widowed" females were able

to raise some offspring successfully (e.g. Weatherhead 1979, Gowaty 1983, Lyon et al. 1987). Only one study found that females could not produce any young without male parental care (Western Sandpiper, *Calidris mauri*; Erckmann 1983). In altricial birds, the ability of unaided females to raise young successfully suggests that most species are monogamous because it is advantageous to females (hypothesis 2) and not to both sexes (hypothesis 1) (Wittenberger and Tilson 1980: 201). However, hypothesis 1 of Wittenberger and Tilson (1980) may explain monogamy in more birds than thought previously because, relative to females, male-removal studies have generally examined species with low levels of male parental care (Fig. 1). There is a need for male-removal studies in monogamous species with varying levels of male parental care so we can better understand the relative importance of male parental care versus other constraints in the maintenance of monogamy (Mock 1985).

We conducted a male-removal experiment designed to evaluate the contribution of male parental care to reproductive success among Black-billed Magpies (*Pica pica*). Black-billed Magpies are monogamous corvids with apparently long-term pair bonds and small differences between

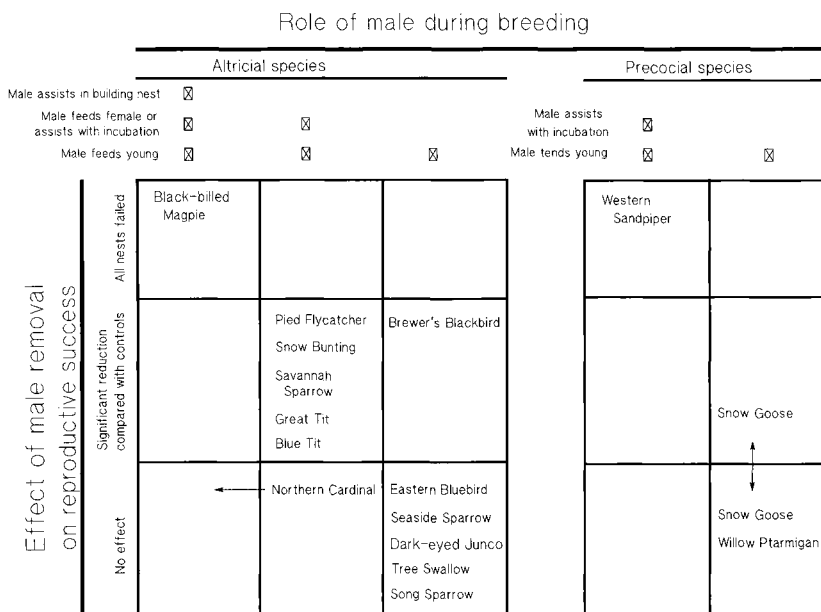


Fig. 1. The distribution of male-removal studies in monogamous birds in relation to male role during breeding (see Appendix for scientific names and references). Data on male role are from Verner and Willson (1969), the male-removal study, or Hochachka (pers. comm., Song Sparrow). Arrows indicate differing results. Behaviors indicate breeding activities of most males of a given species (if data not available from the male-removal study); "X" indicates male participation in that behavior. Reproductive success was compared between control and male-removal groups, using only fledging success, so that estimates of reproductive success would be similar.

the sexes in terms of total energetic investment during breeding (Mugaas and King 1981). The total energetic investments of male and female magpies are similar because males provide most of the food eaten by their mates during incubation, which has a relatively low energetic cost for females (Mugaas and King 1981). Magpies may engage in extra pair-bond copulations, although these appear to be rare, and there is no evidence of subsequent male assistance in these cases (Birkhead 1979, Buitron 1983). In the absence of information on genetically effective matings, we consider that magpies pair monogamously because they maintain a prolonged and essentially exclusive relationship with one partner during the breeding season (Wittenberger and Tilson 1980).

METHODS

The study was conducted on 2 areas in the North Saskatchewan River valley in Edmonton, Alberta, Canada, during April through June 1985-1987. One study area included Kinsmen and Queen Elizabeth parks, and the other study area was Riverside Golf

Course. In 1987 we included magpie nests on the University of Alberta campus and in a nearby residential area (Campus-Windsor Park). The general habitat types were similar to those described by Hochachka and Boag (1987).

Nests were checked at least three times each season to determine laying date (date of clutch initiation), clutch size, and number of young fledged. Laying date was determined directly for nests by inspection before and during laying, and by back-dating from the observed number of eggs (assuming that one egg was laid per day, plus a 1-day gap at some point in laying; Hochachka 1985: 12). Fledging success was taken to be the number of young in the nest at 20 days of age (ca. 1 week before fledging). Nestling age was determined from a known hatch date or by calculating nestling age from a logistic growth equation for bill depth (Scharf unpubl. data). In 1987, nestlings of known age were weighed to determine if young in nests of unaided females grew more slowly than young in nests of paired females. Nest failure was indicated by the loss of all eggs or young.

We observed nests approximately once per week from mid-April to late-May between 0800 and 1800. Observers watched nests from ca. 20 m. This was closer than most previous studies. However, because magpies in the city of Edmonton have habituated to

heavy human activity, we do not believe that our presence influenced their behavior. Each observation session consisted of ten 3-min periods (each period separated by ca. 3–5 min) in 1985 and one 60-min period in 1986 and 1987. An initial nest was chosen randomly every week, after which nests were observed systematically during that week. The time of day that control and unaided females were observed did not differ during the incubation or nestling periods ($t = -0.03$, $df = 11$, $P = 0.98$ for incubation; $t = -1.64$, $df = 11$, $P = 0.13$ for the nestling period; times were arcsine transformed). During each observation period, observers recorded the total number of trips inside the nest by both males and females (feeding trips could not be distinguished from other trips) and the length of time control and unaided females spent on the ground (mostly foraging), in trees, and on the nest. We observed unaided females for 85 h and controls for 108 h. Our analyses, however, were confined to 81 h (unaided) and 33 h (control) of observation, because males and females could not be distinguished reliably at control nests where neither bird was marked individually and because of missing data for some behaviors. Therefore, our observations at control nests come only from pairs in which one or both birds were marked with unique combinations of plastic, colored leg bands.

Within each study area, territories were chosen randomly for removal of males. Territories where males were removed in previous years were excluded. Magpies were caught with an array of fishing-line nooses attached to wire wickets sunk into the ground around a live, decoy magpie (Scharf 1985a). Birds were classified to age (yearling or adult) based on the length of the black tip of the 10th primary (Scharf 1985b) and to sex based on wing length and beak size (Scharf 1987). Classification of age based on the length of the black tip of the 4th primary (Erpino 1968) was inaccurate in this population (Scharf 1985b). Magpies were removed to an aviary. Males assigned for removal were not marked before capture; the territorial status of captured males was determined by location prior to capture (the removal nest or another territory), response of the female toward the male that was caught (before and during capture attempts), and by the presence of other birds on the territory immediately after capture of males presumed to be territory holders. We assumed that we had caught the territory holder if no other bird was seen with the female at the removal nest on the day of capture. When males assigned as controls could be caught, they were measured, color-banded, and held for 30 min before release. This controlled for the possibility that female magpies might desert their nest immediately if males disappear for short periods of time. Because females did not desert nests within one day of banding of their mates or immediately after their own banding, we do not believe that capture and banding caused any of the observed nest desertions.

Laying date and clutch size of control and male-

removal (unaided) females were compared with two-way ANOVAs (main effects were treatment and study area) each year to determine if there were any a priori differences that may have biased the fledging success results. Laying date and clutch size were distributed approximately normally; however, fledging success of all nests (both male-removals and controls) was not distributed normally because of nest failures (zero fledging success) among the male-removal group. The ten 3-min observation periods during each observation session in 1985 were combined and multiplied by 2 to make nest-visit rates equivalent to the 60-min observation sessions in 1986 and 1987. To analyze nest-visit data, we first calculated a mean rate of visits for each nest from multiple observations to obtain independent samples. These means were calculated separately for the incubation and nestling periods. Individual means for each nest were then analyzed with two-way ANOVAs in which the main effects were treatment and year. The year effect controlled for the difference in length of observation sessions between 1985 and 1986–1987. Multi-way ANOVAs were performed with the General Linear Models procedure of the Statistical Analysis System (SAS Institute 1982), and tests of significance were based on the Type III sums of squares (used with unbalanced designs). Statistical tests were all two-tailed and were considered significant at the 0.05 probability level. Means are presented with their standard errors.

RESULTS

We trapped 29 male magpies at 28 nests chosen for removal of males (a territorial male and a replacement male were trapped at the same nest in 1987). We tried to remove 50% of the males during laying or early incubation and the other 50% during late incubation. However, difficulties in trapping males led to a removal schedule of 2 prior to laying, 19 during laying or the first half of incubation, and 5 during the last half of incubation or early post-hatch. In addition, two more males were removed from their territories, but the nesting stage was not known at the time of removal. We could not remove additional territorial males because magpies on most territories did not usually approach the decoy and nooses after three trapping attempts or during late incubation.

After the removal of presumed territorial males, replacement males assisted territorial females at 9 of 28 nests (32%). All of these replacement males defended the nest against intruders (other magpies or human observers) or fed the female at least once. Females were not observed with another male for at most 5–13 days after removal at 7 of these nests and for a

TABLE 1. Reproductive parameters ($\bar{x} \pm SE$) of Black-billed Magpies at control and male-removal nests with and without replacement males. Renests are excluded; the number of nests are in parentheses.

Year	Treatment	Laying date	Clutch size	Fledging success ^a
1985	Controls	20 Apr \pm 1.3 (23)	6.0 \pm 0.3 (26)	2.3 \pm 0.4 (26)
	Male removals			
	Aided ^b	23 Apr \pm 5.2 (5)	6.8 \pm 0.5 (5)	2.2 \pm 0.9 (5)
	Unaided	22 Apr \pm 3.2 (7)	6.9 \pm 0.3 (7)	0.0 \pm 0.0 (7)
1986	Controls	18 Apr \pm 1.5 (20)	5.9 \pm 0.5 (14)	0.9 \pm 0.2 (25)
	Male removals			
	Aided ^b	19 Apr (1)	3.0 (1)	0.0 (3)
	Unaided	23 Apr \pm 4.9 (3)	5.3 \pm 1.2 (3)	0.0 (3)
1987	Controls	18 Apr \pm 0.9 (32)	6.8 \pm 0.2 (26)	1.6 \pm 0.3 (55)
	Male removals			
	Aided ^b			
	Unaided	20 Apr \pm 1.8 (9)	6.7 \pm 0.5 (7)	0.0 (10)

^a Number of young fledged per female; includes nest failures.

^b Aided females were "widows" that gained a replacement male.

maximum of 2 days at the other 2 nests. We analyzed 8 of these 9 nests separately for the effect of replacement males on fledging success. The remaining nest was included in the sample of unaided females because we were able to remove the replacement male (a yearling) <5 days after it appeared. Except for this nest, our repeated attempts to remove replacement males were unsuccessful. Another potential case of replacement involved a male (color code RAOG) neighbor that was seen near the nest of an unaided female in 1987. This male was not considered a replacement, however, because it did not appear to assist the female (during 11 h of observation). Replacement males were seen at both nests where the male was removed prior to laying, at 2 of 19 nests where males were removed during laying or the first half of incubation, at 2 of 5 nests where males were removed during the second half of incubation or within 2 days of hatching, and at both nests where the stage of nesting was not known at the time of male removal.

Unaided females.—We examined laying date and clutch size at control nests and nests of unaided females to see if there were any a priori differences to bias comparisons of fledging success. Laying date for the first egg in a clutch and clutch size (Table 1) did not differ between control nests and nests of unaided females nor among study areas in any year (two-way ANOVAs for each year, main effects were treatment and study area; $P > 0.09$ for laying date each year; $P > 0.11$ for clutch size each year). The fledging-success data could not be tested for differences among years and study areas using

data from nests of unaided females because these data were not distributed normally (all nests failed). Therefore, we tested for study area and year effects with data from control nests only. We also excluded 1987 data from the campus study area in order to avoid empty cells in the two-way ANOVA design. When only control nests were examined, there was a significant difference in fledging success among years (two-way ANOVA, main effects were year and study area; $F = 4.38$, $df = 2, 72$, $P = 0.016$), but there was no difference among study areas ($F = 2.84$, $df = 1, 72$, $P = 0.096$). Inspection of the least-squares means for each year indicated that the difference among years was due to a low fledging success in 1986 (see also Table 1).

TABLE 2. Nesting attempts by Black-billed Magpies that fledged at least 1 young successfully (S) or failed (F) to produce young.

Study area/ year	Unaided females		Control		P^a
	F	S	F	S	
Kinsmen & Queen Elizabeth parks					
1985	4	0	7	5	0.118
1986	1	0	5	0	1.0
1987	4	0	2	5	0.006
Riverside Golf Course					
1985	3	0	2	12	0.004
1986	2	0	8	12	0.159
1987	1	0	6	14	0.286
Campus-Windsor Park					
1987	5	0	21	7	0.228

^a The probability (P) of finding the observed number of nest failures at nests of unaided females among all control nests in a given study area and year (randomization test, see text for explanation).

No young fledged from the 20 nests where females were unaided (Table 1), while the rate of nest failure for all control nests was 48% (51/106 nests; Table 2). We tested whether nests of unaided females failed at a significantly higher rate than control nests by using a randomization test (Sokal and Rohlf 1981) that estimated the probability of finding the observed number of nest failures at male-removal nests among a randomly chosen sample (of equal size) of control nests in the same year and study area. Ten thousand random samples (size of each sample was equal to the number of nest failures at male-removal nests) were drawn with replacement from control nests in each corresponding year and study area to calculate the probability values (Table 2). Of these simulations, 2 of 7 had a significant outcome ($P \leq 0.05$), i.e. the observed rate of nest failure among male-removal nests would not be expected by chance alone (for a given study area and year category). An overall probability value was estimated by comparing the number of significant results ($n = 2$) with a binomial expectation based on the total number of tests made ($n = 7$; table D.30 in Zar 1974). The probability that 2 tests (each with a probability of 0.05 or less) would be significant (out of 7 tests altogether) is 0.04. Therefore, we conclude that even though our sample sizes for male-removal nests were low, the failure of all 20 nests would not be expected by chance.

Time of nest failure was known in relation to hatch for 13 nests of unaided females (only nests in which the male was removed before the latter half of incubation); of these, 7 nests were lost or deserted after hatch (54%). Nests of control birds had a similar pattern: 9 of 16 nests failed after hatch (56%; $G = 0.04$, $df = 1$, $P > 0.75$). The maximum number of days between male removal and nest failure (our nest checks were not made often enough to determine the exact date of failure) averaged 22.2 ± 2.1 days ($n = 20$ nests). The timing of male removal (relative to hatch date) and time to failure of the nest were unrelated (midpoints of ranges were used when exact dates were not known; $r^2 = 0.04$, $df = 19$, $P = 0.38$). We found little direct evidence of predation on nests (2–10% of nests; Table 3): the cause of most nest failure was unknown (75–86%). More nest failures appeared to be associated with spring snowstorms (20–39%) than with predation (Table 3). Body mass of nestlings <4 days old was similar between nests of unaided (13.8 ± 0.3 g, $\bar{x} \pm SE$, $n = 11$

TABLE 3. Causes of total nest failure in Black-billed Magpie nests.

Treatment	Predation ^a		Desertion of nest ^b		Unknown		Total ^c	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Control	3	1	17	6	81	29	100	36
Unaided female	10	2	15	3	75	15	100	20

^a Feathers or cracked eggs were found in or near the nest.

^b Cold eggs or dead young were found in the nest. This could also have been due to predation on the female parent.

^c Thirty-nine percent ($n = 14$) of control nests and 20% ($n = 4$) of nests of unaided females failed within 2 days of a snowstorm.

nestlings) and paired (13.6 ± 1.1 g, $n = 38$) females ($t = 0.18$, $df = 47$, $P > 0.5$), but at 5–9 days of age, body mass was lower in nests of unaided (24.1 ± 1.2 g, $n = 8$) than paired (42.9 ± 4.2 g, $n = 22$) females ($t = 4.16$, $df = 28$, $P < 0.001$). Most nests of unaided females failed after nestlings reached 9 days of age, so we do not have any data for later ages. Although our data are limited, we believe that starvation may have been the cause of nest failure when males were removed.

We thought that unaided females would change their behavioral patterns to compensate for the loss of male parental care. However, we found no differences between unaided and paired females in the total time sitting, time spent in the nest, or time spent on the ground (Table 4). During both the incubation and nestling periods, number of nest visits per hour did not differ between unaided and paired females, although there was a trend ($P = 0.09$) toward more nest visits by unaided than paired females during incubation (Table 4). During incubation, the total rate of visits at control nests (i.e. both the male and female) was 1.8 times the rate at nests of unaided females, and during the nestling period it was 2.4 times the rate at control nests (Table 4). The difference in total nest-visit rate during the nestling period was not due to differences in the age of young in nests of unaided versus paired females (7.9 ± 2.1 days old in control nests, 8.9 ± 2.0 days old in nests of unaided females; $t = 0.36$, $df = 14$, $P > 0.5$).

"Widows" with replacement males.—Females with replacement males produced as many fledglings as control females in 1985 ($t = 0.1$, $df = 29$, $P > 0.9$), but in 1986 females with replacement males produced fewer fledglings (Table 1), although the sample size was too small

TABLE 4. Behavior of Black-billed Magpies at control and male-removal nests ($\bar{x} \pm SE$). Observations of nests of unaided females during incubation include only nests at which the male was removed during laying or early incubation. Times are out of 1 h (in min). Time spent flying and moving in trees was not included; total time sitting includes time spent on the nest. The number of nests is in parentheses.

Period/ treatment	Total observ- ation time (h)	Nest visits per hour		Females only		
		Total	Female only	Total time sitting	Time in nest	Time on ground
Incubation						
Control	26	2.5 \pm 0.4 (9)	0.8 \pm 0.2 (9)	51.7 \pm 4.2 (9)	43.1 \pm 6.5 (9)	2.2 \pm 1.4 (9)
Unaided females	69	1.4 \pm 0.2 (13)	1.4 \pm 0.2 (13)	53.0 \pm 2.3 (13)	45.6 \pm 3.7 (13)	2.7 \pm 1.4 (13)
P^a		0.002	0.09	0.53	0.74	0.81
Nestling						
Control	7	4.4 \pm 1.7 (6)	1.6 \pm 1.2 (5)	42.5 \pm 6.8 (6)	22.5 \pm 11.0 (5)	8.5 \pm 5.6 (6)
Unaided females	12	1.8 \pm 0.4 (7)	1.8 \pm 0.4 (7)	45.0 \pm 5.6 (7)	38.0 \pm 10.6 (4)	10.7 \pm 3.9 (7)
P^a		0.02	0.95	0.92	0.91	0.99

^a Probability of no difference between behaviors at nests of control and unaided females. Probability values are from a two-way ANOVA (main effects were treatment and year). All interactions were nonsignificant.

for testing in 1986 (the one replacement male in 1987 was removed). When replacement males assisted females, nest failure rates were 20% (1/5) in 1985 and 100% (3/3) in 1986, compared with rates of 35% (9/26) and 52% (13/25) at control nests in 1985 and 1986, respectively. It appears that unaided females with replacement males can produce as many, or almost as many, offspring as control females. However, except for the potential replacement male in 1987 (male RAOG), we never observed males associating simultaneously with a widowed female and another female, and we did not know the breeding status of replacement males. If male RAOG were breeding simultaneously with two females, then he would have produced fewer fledglings than monogamous males, because RAOG produced one fledgling at his original nest and no offspring were produced at the nest of the unaided female that he visited.

DISCUSSION

In contrast to almost all other male-removal studies, female Black-billed Magpies that lacked male assistance were not successful in raising any young. This indicates that male parental care is more important in Black-billed Magpies than in any other passerine in which males have been removed experimentally (Fig. 1). Buitron (1988) found a similar effect of loss of male parental care on fledging success in two cases when

males disappeared before fledging. After fledging, however, two unaided birds (1 male and 1 female) raised 4–6 young to independence (Buitron 1988). It should be noted that our conclusions depend on two assumptions. First, possibly our sample of unaided females was not a random sample of the entire population but only of those females that were not able to attract a replacement male. The females that gained a replacement male may have been better quality parents, and they may have been able to raise offspring alone. Our evidence to suggest that this was not true came from the one widowed female that gained a replacement male but subsequently failed to produce any young after we removed the replacement male. To our knowledge, there is also no evidence that characteristics related to a female's ability to attract mates is correlated with quality as a parent. Second, our results do not necessarily indicate that an absolute need for male parental care maintains monogamy in magpies, as implied by hypothesis 1 of Wittenberger and Tilson (1980). Hypothesis 1 would only apply if monogamy were advantageous to both sexes. There is still the potential for male magpies to produce more offspring by aiding two females, if two females can each produce some offspring with a fraction of the male's total parental care. We use data from our study and others to argue below that monogamy is advantageous to male magpies.

Information on replacement males that were

neighbors could suggest whether males can successfully split their parental care between two females. We found no evidence that replacement males were neighbors. However, only one of eight widows with replacement males had a neighbor that was banded. A potential replacement male (RAOG) was seen at more than one nest, but he assisted only the female on his original territory. Even assuming that male RAOG was bigamous, this male would not have increased his fledging success above that of monogamous males. We suspect that most replacement males came from flocks of nonbreeding magpies present throughout the breeding season.

We could find no other reports in which male magpies increased their reproductive success by splitting their parental care between two nests. Baeyens (1981a, pers. comm.) reported two cases of "bigamy" that arose when males were captured and a neighboring male annexed the territory and remaining mate. However, the eggs were rotten or the young were dead in the neighboring male's nest, so these cases might be considered renesting attempts rather than simultaneous "bigamy." In addition, no eggs were laid during these new associations and the former pair bond was restored when the captive males were released (after 4–18 days). In cases where males disappeared before eggs were laid, replacement males bred successfully with the unmated females (Baeyens 1981a, pers. comm.; see also Buitron 1988). Therefore, although Black-billed Magpies may mate with more than one bird in a breeding season, it appears that "bigamy" is performed sequentially (after nest failure) rather than simultaneously. Even in cases where replacement males may have bred simultaneously with two females, they were no more successful than monogamous males (Baeyens pers. comm., this study). In summary, monogamy is probably advantageous to both male and female magpies because completely unaided females produce no offspring, and males do not appear to profit from polygyny. To our knowledge, this is the first experimental evidence reported for obligate male parental care in a passerine.

If reproductive success invariably falls to zero following male removal, then one might hypothesize that unaided females should desert their nest or attempt to gain a new mate. Instead of deserting immediately, "widows" remained at their nests for more than 2.5 weeks after mate

removal (see also Baeyens 1981a, Shannon 1958). These females might remain at the nest if gaining a replacement male at the first nest is less costly (in terms of reproductive success) than renesting. Successful renesting is still possible throughout the nestling period in this population (mid-May to early June; e.g. 73% [8/11] of renests were successful in 1987; cf. Erpino 1968b). Nevertheless, 68% (19/28) of all unaided females did not gain a replacement male and ca. 50% continued to nest until hatching. We cannot explain why these females did not desert their nests earlier. Replacement males may become more available later in the breeding season (after other nests fail) or it may be possible for unaided females to raise a few offspring in years of high food abundance (Lyon et al. 1987).

Behavioral observations suggested that unaided females were not able to compensate significantly for the loss of male parental care. Before and after hatch, unaided females made fewer visits to the nest than the total visits of both the male and female in control pairs. This difference is likely due to the male's provision of most of the incubating female's food and the increasing participation of females in nest visits as the nestling period progresses (Buitron 1988). During incubation, control and unaided females spent similar amounts of time in the nest (71–76%) and on the ground (4–5%). Buitron (pers. comm.) found that an unaided female made more feeding trips and had a lower nest attendance rate when her mate disappeared during incubation. Our results are similar. Unaided females tended to increase their rate of nest visit, but we cannot explain the lack of difference in nest attendance between unaided and control females. Unaided females may compensate for the loss of male feeding by foraging more often while they are on the ground; however, we did not record direct measures of feeding rate. Buitron (1988) reported an increase in feeding rate by an unaided female when its mate disappeared two days after the young fledged. This increased feeding rate was still lower than it was when both parents were present. In contrast to Buitron (1988), we may not have found an increase in the nest-visit rate of unaided females during the nestling period because the birds we observed had young nestlings (mean = 7 days old), and they may have spent more of their time brooding the young. Females may spend >60% of their time in the nest during the early nestling period (Erpino

1968b, 67%; Buitron 1988, 72%). We found that, whereas unaided females spent a similar percentage of time in their nests (63%, Table 4), control females spent only 38% of the time in their nest. The small sample size in this study for control nests during the nestling period may be the cause of the discrepancy among studies.

Male parental care is essential.—Buitron (1988) suggested that male and female magpies were so specialized in their types of parental care that both parents were needed to produce offspring. This may be true in terms of physiological adaptations for incubation and brooding (e.g. the male has no brood patch). Magpies, however, can alter the rate of food delivery to nestlings (Buitron 1988) and the nest-visit rate during incubation (Buitron pers. comm., this study). One major role of males may be to supply incubating and brooding females with most of their food (Baeyens 1981a; pers. obs.). Adding food increases the number of young that leave successful nests (i.e. nests that produce at least one fledgling), although it did not decrease the rate of nest failure in this population (Hochachka and Boag 1987). Although our data are limited, young in nests of unaided females weighed less and starvation may have been the cause of nest failure among unaided females. We found no difference in the cause of nest failures between unaided and paired females. The cause of nest failure was unknown in most cases. Spring snowstorms may contribute to many nest failures (Table 3; cf. Buitron 1983b: 225). Male parental care may also be important in magpies to protect eggs and young against predators (Baeyens 1981b, Buitron 1983b). However, nest predation did not appear to be the major cause of total nest loss in this study (3–10%) or others (mean = $27 \pm 6\%$, $n = 6$ populations; Baeyens 1981b, Tatner 1982, Balança 1984, Reese and Kadlec 1985, Buitron 1988). Total nest failure from all causes may be a major limiting factor in magpie reproduction (mean nest failure rate = $46 \pm 4\%$, $n = 14$ populations; Hogstedt 1980, Baeyens 1981b, Vines 1981, Møller 1982, Tatner 1982, Seel 1983, Balança 1984, Eden 1985, Hochachka 1985, Reese and Kadlec 1985, Buitron 1988). Although we are not sure of the cause of nest failure in this study, it may be possible to determine why male parental care is so important by examining the mechanism of nest failure in greater detail.

There is no general consensus as to why male removal has a significant effect on reproductive

success. Several authors have suggested that feeding nestlings may be the primary benefit of male parental care (Alatalo et al. 1982, Bjorklund and Westman 1986, Lyon et al. 1987). This conclusion was based on a lower body mass at fledging among the young of unaided females. However, feeding ability may not be the ultimate cause of lower reproductive success if unaided females have to spend more time in other activities (e.g. predator defense) that subsequently reduce feeding rate. This possibility, plus the potential for interactions between feeding rate and predation (Wolf et al. 1988), indicates that only carefully designed experiments can determine why male parental care is important.

Male parental care and monogamy in other species.—If, among species, female reproductive success is correlated positively with male parental care, then one may expect to find a greater reduction in reproductive success after male removal in species with relatively greater male parental care. This relationship is not clear-cut (Fig. 1), although there is a mild trend toward greater loss of reproductive success among species in which the male contributes to building the nest, incubating (or feeding the female while she incubates), and feeding nestlings than among species in which the male mainly feeds or tends the young (Fig. 1). The argument may be confounded by differing times of male removal in each study. The effect on reproductive success was not associated with the period of male removal in these studies (removal periods were laying, incubation, and nestling: $G = 0.79$, $df = 2$, $P = 0.67$). The effect of male removal on reproductive success may also be influenced by the relative extent of male investment in each breeding activity, rather than just whether or not the male assisted in a particular activity. A more quantitative and less arbitrary way to compare species (and to predict where they may fit into the scheme in Fig. 1) may involve estimating energy expenditure of males and females during breeding (e.g. Mugaas and King 1981, Beissinger 1987). However, energy expenditure may be a biased estimator of parental investment if males engage in risky behaviors (e.g. predator defense) that may be relatively low in energy expenditure (see also Bryant et al. 1984).

Wolf et al. (1988) have reviewed male-removal studies of passerines. They concluded that male removal had the greatest effect on repro-

ductive success in species that nested in cavities or bred at higher latitudes. Both are correlated with larger clutch sizes. Species with larger initial clutch sizes might benefit relatively more from male parental care because the value of male parental care is greater with larger clutches (Patterson et al. 1980). Data from studies in our Fig. 1 suggest an almost significant trend toward larger clutch size among passerine species with a significant decrease in reproductive success following male removal (4.3 ± 0.5 eggs, $n = 5$ studies vs. 6.9 ± 1.1 eggs, $n = 6$ studies; $t = 2.2$, $df = 7$, $P = 0.064$). This trend may not continue with species that always fail after male removal; magpie clutch size in this study averaged 6.2 eggs.

Our study and the study by Wolf et al. (1988) indicate gaps in understanding what factors maintain monogamy in different species and populations of birds. Patterns of male parental care will not completely explain monogamy (e.g. Fig. 1). However, an understanding of how male parental care varies across monogamous species and why it is important in each species will reveal the relative importance of other constraints (e.g. breeding synchrony, environmental variability, variance in territory quality) on breeding behavior.

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APPENDIX. Scientific names and references used in Figure 1.

Snow Goose (*Anser caerulescens*), Martin et al. 1985; Western Sandpiper (*Calidris mauri*), Erckmann 1983; Willow Ptarmigan (*Lagopus lagopus*), Hannon 1984, Martin and Cooke 1987; Pied Flycatcher (*Ficedula hypoleuca*), Alatalo et al. 1982; Tree Swallow (*Tachycineta bicolor*), Dunn unpubl. data; Black-billed Magpie, this study; Blue Tit (*Parus caeruleus*), Sasvari 1986; Great Tit (*Parus major*), Sasvari 1986, Bjorklund and Westman 1986; Eastern Bluebird (*Sialia sialis*), Gowaty 1983; Northern Cardinal (*Cardinalis cardinalis*), Richmond 1978; Savannah Sparrow (*Passerculus sandwichensis*), Weatherhead 1979; Seaside Sparrow (*Ammodramus maritimus*), Greenlaw and Post 1985; Song Sparrow (*Melospiza melodia*), Smith et al. 1982; Dark-eyed Junco (*Junco hyemalis*), Wolf et al. 1988; Snow Bunting (*Plectrophenax nivalis*), Lyon et al. 1987; Brewer's Blackbird (*Euphagus cyanocephalus*), Patterson et al. 1980.
