FEMALE AND MALE SPECIALIZATION IN PARENTAL CARE AND ITS CONSEQUENCES IN BLACK-BILLED MAGPIES[1]

Deborah Buitron[2]

*Bell Museum of Natural History, Department of Ecology and Behavioral Biology,
University of Minnesota, Minneapolis, MN 55455*

Abstract. The breeding biology of a small population of individually marked Black-billed Magpies (*Pica pica*) was studied from 1978 through 1981 in Wind Cave National Park, South Dakota. Mates cooperated extensively in nest building, defense of nest site, and care of eggs, nestlings, and fledglings. The two sexes specialized in different types of parental care, with the result that both parents were needed to fledge young. Of the types of parental care that I was able to measure, males contributed more than females to raising young and were also more active in expelling intruders and driving away predators. Feeding of young peaked the week after fledging and parental care continued for another 5 to 6 weeks. Individual variability in parental behavior and two cases of the care of young by unrelated adults are also discussed.

Key words: Black-billed Magpies; Pica pica; *parental care; individual variability.*

INTRODUCTION

Black-billed Magpies (*Pica pica*) are monogamous birds that frequently retain their mates for several years. Parental care is extensive and prolonged, and females and males have specialized to provide different types of care. In this paper I examine how female and male Black-billed Magpies cooperate to raise young by quantifying the contributions of each sex, variability in the behavior of individual pairs, and factors that might influence individual differences.

Magpies are widely distributed over the northern hemisphere and, like most corvids, show flexibility in their behavior (Goodwin 1976). There is some indication from previous studies in North America (e.g., Linsdale 1937, Brown 1957, Erpino 1968a) and Europe (e.g., Goodwin 1976; Baeyens 1979, 1981a, 1981b, 1981c; Birkhead 1979; Högstedt 1981a, 1981b; Vines 1981; Birkhead et al. 1986) that nesting behavior of individuals varies among different populations, making comparisons between habitat types rewarding. So far there has been little detailed information on variability in the parental roles of males and females, either between pairs or in different stages of the breeding cycle. In addition, few data are available from any population on the division of labor in certain aspects of parental

care such as nest building or the care of young once they have left the nest.

METHODS

The study area consisted of 6.3 km² of rolling prairie with scattered clumps of ponderosa pines (*Pinus ponderosa*) located in Wind Cave National Park, in the Black Hills of South Dakota. Adult magpies (*n* = 40), trapped with monofilament nooses hidden in grass around bait (e.g., suet), and nestlings (*n* = 176) were marked with numbered aluminum leg bands and unique combinations of plastic, colored leg bands. Breast feathers were dyed yellow with picric acid or black with Nyanzol D. Birds were weighed with 300-g and 500-g Pesola scales, and the length of the black tip of the fourth primary was used to identify yearlings (Erpino 1968b). The study began in mid-April 1978. From 1979 through 1981, I arrived the last week in February and remained until August.

Pairs were watched from 100 to 300 m distance with 7 × 50 binoculars or a 15–60× telescope. The same locations were used for observation each day to minimize disturbance to the magpies. My assistants and I attempted to watch each pair 1 to 3 hr daily from March through July. The daylight hours were divided into three 5-hr periods with observations scheduled so that after 3 days each pair had been watched once in each time period. Several all-morning (6 hr) and all-day (15 hr) watches on pairs were made during the nestling and fledgling stages.

During observations, continuous written records were kept of a pair's foraging behavior, social interactions, and responses to other species. Nests were checked 3 to 4 times over a 40-day period. No desertions appeared to be caused by these visits (during which we wore disguises after the first year) or by our observations. I determined the beginning of laying by checking a nest for eggs when the female began both begging and spending long periods of time in her nest. Later, nests were checked to confirm that eggs had hatched, and when nestlings were 17 days old they were banded. Data were analyzed using chi-square tests, sign tests, paired t-tests, t-tests for samples with unequal variances, and one-way analysis of variance (Snedecor and Cochran 1980). Except where otherwise indicated, t-tests were one tailed.

RESULTS

NESTING ECOLOGY

Twelve to 16 pairs of magpies bred each year, and 64 to 79% of the individuals were marked. Four marked birds, including one pair, nested in the area all 4 years, and 19 individuals were present at least 2 years. Of 126 banded young fledged between 1978 and 1980, one male and two females returned to breed as yearlings, while two other males returned as 2-year-olds. Of the 66 breeding birds for which ages were known, six were yearlings (9%). Males were 24% heavier than females (males: 188–232g, $\bar{x} = 203.7$, SD = 10.1, $n = 10$; females: 147–179g, $\bar{x} = 163.6$, SD = 10.0, $n = 13$, $t = 9.49$, $P < 0.001$). Of the five males and four females whose mates were killed or disappeared, two males obtained new mates within 24 hr. Two females had new mates within 1 month, and the remaining five adults did not acquire mates that breeding season.

Nest sites and food. Nests were located primarily in clumps of trees and bushes close to sources of water and food, such as picnic areas and highways, where roadkills were common. Nests were 65 to 650 m apart ($\bar{x} = 300$, $n = 56$) and an average of 8.6 m (1.5 to 16 m) above the ground. Fourteen of 56 nests had been used before, but only three during the previous year. All 136 nests located in the park and on neighboring ranches had domes.

Pairs nested in the same area year after year, moving an average of 280 m from their previous nest (range = 0–790 m, SD = 268, $n = 20$). There was no apparent correlation between the distance moved each year and whether a nesting attempt the previous year had been successful, or whether mates had been changed. Food consisted of insects, primarily grasshoppers (Orthoptera), and road-kills, mostly prairie dogs (*Cynomys ludovicianus*). Small bullsnakes (*Pituophis melanoleucus*), rodents, and young cottontails (*Sylvilagus floridanus*) were also killed.

Territoriality and dominance. Nesting pairs excluded birds only from an area within 30 m from a nest, but dominated other magpies within an area of about 3 ha. Except during incubation, when females rarely left their nests, females and males were about equally active in nest-site defense. Usually males expelled intruding males and females expelled females, but sometimes both chased a single intruder.

Foraging areas overlapped widely, and often two or more pairs searched for insects side by side. Dominance and aggression were much more common at a concentrated food source, such as a road-kill. At road-kills the pair whose nest was closest to the food dominated other magpies, and within a pair the male dominated the female. However, by begging loudly, laying or incubating females often displaced both their mates and even the locally dominant males from desired food.

During the nonbreeding season, pairs frequently foraged over 1 km from their nests, and nest sites were not occupied from mid-July until mid-September. Even when eggs or young were present the male was often 0.5 km away. Breeding magpies joined nonbreeders at communal roosts over 1 km from their nests, except when incubating eggs and brooding young nestlings.

Clutch sizes. Clutches had 4 to 9 eggs, with an average of 6.2 (SD = 1.1, $n = 31$). One-year old females laid smaller clutches but did not fledge fewer young than older females (Table 1). Females of pairs that had bred together previously laid larger clutches than newly paired, nonyearling females, yet fledged about the same number of young (Table 1). Of 56 pairs that attempted to breed between 1978 and 1981, 34 fledged 4.4 young/pair (SD = 1.7), or 2.5 fledglings per nesting pair. A clutch of four eggs and a clutch of five eggs were laid as replacement clutches 14 days following nest failure, but the one young to fledge died within 1 week. There were no significant trends between clutch size and date of laying.

Hatching and feeding of nestlings. Eggs hatched

TABLE 1. Mean clutch size and number of young fledged in relation to female age and length of pair bond. Values for *t*-tests with unequal variances are included.

	Clutch size			Young fledged/nesting pair		
	No. pairs	$\bar{x} \pm$ SE	*t*	No. pairs	*t*	$\bar{x} \pm$ SE
Female age (years)						
1	4	5.3 ± 0.4	2.6*	4	1.6	1.0 ± 0.6
≥2	13	6.6 ± 0.3		13		2.5 ± 0.7
Length of pair bond (years)						
1	8	5.9 ± 0.4	1.8*	10	0.2	2.0 ± 0.8
≥1	5	6.9 ± 0.4		9		1.8 ± 0.8

* Significant at the 0.05 level.

18.6 days after the last egg was laid (SE = 0.02, range = 17–21, n = 27 clutches). Hatching was asynchronous and, in clutches of six or more, occurred over 2 or 3 days. Nestlings fledged after 23 to 32 days ($\bar{x}$ = 27.2, SD = 2.2, n = 20). The highest feeding rates occurred before noon and the lowest in mid-afternoon (Table 2).

The feeding rate by both parents combined increased from 0.7 trips/hr/young on day 3 to a peak of 1.8 trips/hr/young on day 39 (Fig. 1). Only three to four families could be watched from day 50 to 60, but in these the adults were still feeding their offspring on day 60, at about 0.3 to 0.4 times/hr.

Care of fledglings. Young remained in the cluster of trees and bushes near the nest for a week or two after fledging, while parents resumed spending the night at the communal roost. A minimum of 23/106 young (22%) disappeared during this 2-week period. Within 9 to 29 days of fledging, families began moving more widely, and groups of two to eight families joined together in sheltered areas near water and good foraging. Fledglings began following their parents each night to the roost.

Within these mixed family flocks, siblings usually remained close together. Although young

begged from all adults, parents fed only their own offspring. Brood division did not occur. After 3 to 4 weeks, parental feeding decreased, but the adults continued to lead the young and warn them of danger.

Families left the study area the last half of July, 5 weeks after most young had fledged. In 1980 I located five of these marked families and an independent, all-juvenile flock of 40 birds on a ranch 4 km from the study area. The juvenile flock included at least 12 of the young from my study area, by then fledged for 6 weeks. This valley contained abundant grasshoppers, on which the juveniles were feeding almost exclusively.

SEX ROLES AND DIVISION OF LABOR

Some types of division of labor between females and males appeared to be inflexible. In addition to laying the eggs, only females incubated the eggs and brooded young nestlings. When a female was killed or disappeared, her mate did not attempt to incubate eggs or brood nestlings and, if

TABLE 2. Number of trips to the nest by both parents during all-day watches in seven pairs when young were 25 to 31 days old. Mean day of fledging was 27 days.

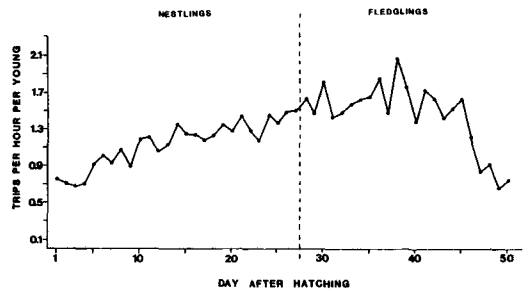| Time	No. trips	$\bar{x}$/hr ± SE
05:31–08:30	228	10.9 ± 0.8
08:31–11:30	195	9.3 ± 0.8
11:31–14:30	157	7.5 ± 0.8
14:31–17:30	102	4.9 ± 0.8
17:31–20:30	122	5.8 ± 0.9
Total	804	7.7 ± 0.4

FIGURE 1. Feeding rates (trips per hour per young) of nestlings and fledglings by both parents from day 1, when the first egg hatched, through day 50. Based on 21 pairs observed for 1,457 hr up to day 45, six pairs for 35 hr after day 45.

TABLE 3.   Trips carrying nest material and time spent working on the nest by females and males. Data based on 304 hr observation of 14 pairs building 16 nests.

Pair	Year	Number of trips			Number of minutes		
		Males	Females	% by females	Males	Females	% by females
NV	1979	45	24	34.8	33	47	58.5
NV[1]	1981	105	86	45.0	118	88	42.8
Y	1980	155	39	20.1	147	89	37.7
Y[1]	1981	184	70	27.6	260	194	42.7
DS	1979	22	29	56.9	29	66	69.7
DS[2]	1980	53	52	49.5	31	75	70.9
RY	1980	150	61	28.9	229	121	34.6
RY[3]	1981	26	28	51.8	49	42	54.4
PI	1980	59	48	44.9	52	54	51.2
PI[3]	1981	59	45	43.3	68	83	55.0
O	1981	129	88	42.5	245	97	28.3
R	1981	345	201	36.8	448	297	39.9
GU	1981	92	56	37.8	109	64	37.0
ER	1981	53	34	39.1	55	43	43.9
FP	1981	145	69	32.2	175	125	41.7
S	1981	153	123	44.6	238	333	58.3
Total		1,775	1,053	37.2	2,286	1,818	44.3

[1] Same pair.
[2] Same female, different male.
[3] Same male, different female.

not already close to fledging or fledged, the young died (five females disappeared or died: three before young fledged, two after). Other types of parental behavior showed considerable flexibility between individuals, such as the division of labor in nest building, and the feeding of mates and young.

Nest building. Nest building began in February, peaked in March, and was most intense during the first 2 to 3 hr of daylight. Most material for a nest was obtained within 20 m, but during

TABLE 4.   Sex differences in types of nest material and size of twigs taken to 16 nests being built by 14 pairs (304 hr observation).

	n	Females (exp)	Males (exp)
Types of material			
Mud	250	51 (71.2)	199 (178.7)
Grass	340	146 (96.9)	194 (243.1)
Twigs	1,332	351 (379.8)	981 (952.2)
Total	1,922	548	1,374
	$\chi^2 = 45.9$, df = 2, $P < 0.005$		
Size of twigs			
<20 cm	390	123 (102.8)	267 (287.2)
20–30 cm	795	196 (209.5)	599 (585.5)
>30 cm	147	32 (38.7)	115 (108.3)
Total	1,332	351	981
	$\chi^2 = 8.2$, df = 2, $P < 0.025$.		

dry periods some pairs repeatedly flew up to 960 m to gather mud at a creek or pond.

Males of 12 out of 14 pairs made more trips carrying nest material than females ($P = 0.01$, Sign test, Table 3), but there was no difference in the time spent working on nests ($P = 0.79$, Sign test). Females were three times as likely to carry grass to the nest than mud, while males showed no preference (Table 4). Males took more medium and large twigs than small twigs ($n = 981$ trips), while the reverse was true for females (Table 4).

Individuals were consistent in how much effort they put into building. Female Y (Table 3) contributed the least proportion of nest material both years, when she was paired to the same male. The female (DS) that contributed the most material (in 1979, paired to the same male as in 1978) also contributed an unusually large amount the following year when she was paired to a new male. During both years this female contributed the greatest percent of time spent nest building (70%), well above the population mean of 44% (Table 3).

I observed two cases of newly-formed pairs working on nests. The first example occurred in 1980 when the DS female disappeared and the 1-week-old nestlings died. The following day the male was accompanied by a new female, and he
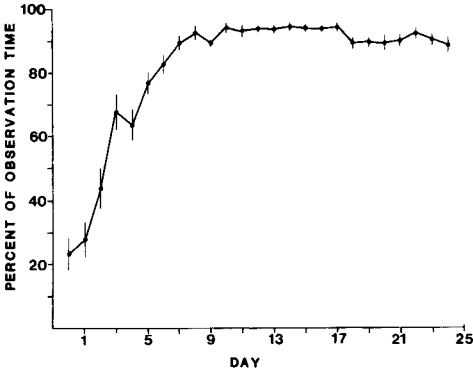
FIGURE 2. Percent of observation time (±SE) females spent in their nests during laying and incubation (18 to 30 pairs, 840 hr observation). The first egg was laid on day 1.

FIGURE 3. Relation between the day a female began laying and (A) when she first begged ($n = 35$ females); (B) when her mate first brought food ($n = 27$ males). The first egg was laid on day 1. Days before laying are indicated with minus signs.

began building a nest 50 m from his previous one. Although the new female remained nearby, she did not contribute any material for 2 days. In all, this female took only 10 of 102 items to the nest (10%), and no eggs were laid. The following year that female was not seen and the male was paired to a new female.

The second case occurred in 1981, when an older female (R) drove away a yearling female that had been working on a nest with her mate for 3 weeks. The male made no effort to help his original mate and quickly accepted the new female. Unlike the previous case, this new female immediately began working on the nest, making more trips and spending more time building than her predecessor.

Contact between mates. During nest building, mates were in almost constant vocal contact and kept close together, often looking for twigs in the same area and waiting for each other before returning to the nest. Mates were in sight of each other 95% of 280 occasions in which at least one member of a pair was located in 1981. Of 79 moves of over 2 m, females initiated 48 (61%) and were immediately followed by their mate on 44 (92%). Males initiated 31 moves and their females followed on 23 (74%). The amount of time a male spent within sight of his mate decreased from over 80% the day before and the day of laying the first egg (days 0 to 1) to less than 40% by the end of laying (day 7, 200 hr observation of 12 pairs, Buitron 1983a).

Egg laying and incubation. As laying progressed, females spent less time feeding and more time incubating (Fig. 2). This percentage in-
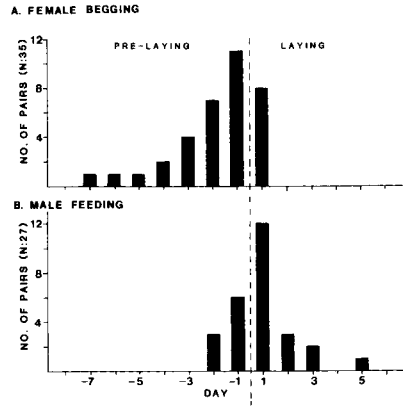
creased from 23% on day 1 to 90% on day 7 and remained at between 90 to 95% until the eggs hatched on day 24 or 25.

Female-demand behavior and mate feeding. Most females began begging loudly from their mates on the day the first egg was laid, or on the two previous days (74% of 35 females, Fig. 3A), though some individuals began up to 7 days before their first egg. In most pairs, males were feeding their mates by the first day of laying (78% of 27 males, Fig. 3B). Female-demand behavior peaked during the first days of laying, and occurred primarily away from the nest (Smith 1980). Females followed their foraging mates for hours at a time, giving the begging call and flapping their wings. On days −1 to +2, females begged from their mates during 40 to 45% of the minutes they were observed in 1981 (Fig. 4). Males often responded by courting their mates. Such courting
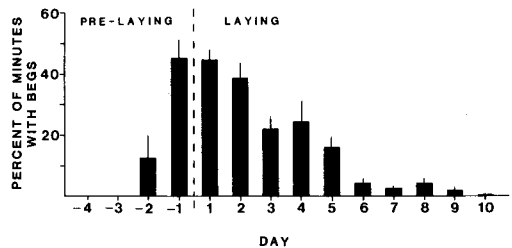

FIGURE 4. Intensity of begging (±SE) by females from their mates as a function of the reproductive stage in 1981 (11 pairs, 135 hr observation).
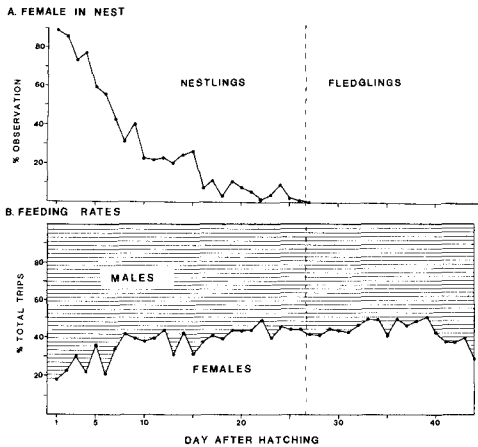
FIGURE 5. Care of young by females. (A) Percent of observation time females were in their nests and (B) proportion of feeding trips to young made by females and males. The first eggs hatched on day 1, young fledged on day 24. Based on 21 pairs observed for 1,457 hr.

TABLE 5. Rates at which females and males fed young at different ages for 12 pairs that fledged four to seven young (928 hr observation). Young fledged after 24 days.

| | Feedings/hr ($\bar{x}$) | | |
	Females	Males	Paired t-test
Day 1–12	1.4	3.1	5.31*
13–24	2.6	3.5	2.52*
25–36	3.0	3.3	1.33
37–48	1.9	2.6	2.09

* Significant at the 0.05 level.

males gave an elaborate series of vocalizations, fluffed their feathers, held their tails at an oblique angle, and tried to position themselves parallel to the female while slowly flapping their extended wings (Baeyens 1979). Only twice during three springs of watching laying birds did I see the female respond by crouching and allowing her mate to mount.

The frequency of female begging decreased to less than 3% by day 7, although feeding rates by the male remained high throughout incubation (see below). By the end of laying, most females begged only when their mates arrived at the nest to feed them.

Only females incubate, and during incubation females rarely foraged even when they left their nest to stretch, preen, and defecate. Males appeared to provide nearly all of their mates' food during the 24 or 25 days of laying and incubation. Although the type of food rarely could be seen, the bulge made by the food in the extendable throat pouch was clearly visible, and appeared to be relatively similar in size from one trip to the next and in different males. Therefore the rate at which males brought food to their mates probably was roughly proportional to the quantity.

Feeding rates were highest during the first few hours of daylight and lowest the last few, but the variability in rate from one hour to the next was great. The mean rate at which males brought food

to their mates was 1.6 times an hour (range: 0–9, $n = 34$ pairs, 914 hr observation) and did not differ significantly during laying and incubation. Newly paired males fed their mates at rates that were significantly higher (1.9 trips/hr, SD = 0.66, $n = 11$) than those of pairs that had previously bred together (1.4 trips/hr, SD = 0.28, $n = 8$; $t = 2.4$, $P < 0.05$, two-tailed).

Brooding of nestlings. Only females brooded nestlings. Brooding was most extensive during the first week after hatching (Fig. 5A), especially when it was cold or raining. After day 15, brooding decreased to less than 10% of the observation time, but occasional brooding continued until the young fledged.

Feeding of nestlings and fledglings. As the amount of time females spent brooding young decreased, the rate at which they fed young as well as their contribution relative to that of the males increased, but the total rate remained significantly less than that of the males until after the young fledged (Fig. 5B, Table 5). For the first week after hatching the rate for females is probably an overestimate because it was sometimes difficult to tell if a female entering a nest had food for the young or was just returning to brood them. When young were 19 to 40 days old, females made an average of 45% of all feeding trips (SE = 0.6, range: 34–62%, $n = 21$) but after day 40, females' feeding rates decreased slightly. I found no difference between the amount of food per trip that males and females fed fledglings. Either parent was as likely to feed one, two, or three young from one load of food, and each brood member was fed by both parents. However, because of their smaller body size, females with full throat pouches may be carrying slightly less food than males. For this reason, females possibly were contributing slightly less food than the proportion of trips suggests.

TABLE 6. Two case histories of feeding-rate adjustment after disappearance of one mate: average number of feeding trips per hour (±SE) during the 5 days before and after a mate disappeared: (A) RY pair, female disappeared 30 days after her seven young hatched, 2 days after they fledged. (B) Gorge pair, male killed 30 days after his five young hatched, 2 days after they fledged. Values for *t*-tests are included.

	A			B		
	Before mate disappeared	After mate disappeared	*t*	Before mate disappeared	After mate disappeared	*t*
Observation periods (*n*)	10	9		6	6	
Hours of observation	10.5	8.5		16	12.5	
Trips/hr	4.8 ± 0.5	6.7 ± 0.6	2.3*	2.2 ± 0.7	4.3 ± 0.7	2.1*
Total trips/hr/young	1.7 ± 0.2	1.1 ± 0.1		1.4 ± 0.3	0.9 ± 0.1	

* Significant at the 0.05 level.

Single parents. Twice a single mate was left as the sole provider of care to its fledglings. In 1980 RY succeeded in raising six of his seven fledglings to independence in spite of the loss of his mate 2 days after the young fledged. After his female disappeared, RY significantly increased the rate at which he fed his young from 4.8 trips/ hr to 6.7/hr (Table 6A). The reciprocal situation occurred in 1981, when a male was killed by a falcon 2 days after his young fledged. His mate almost doubled the rate at which she brought food to her young (Table 6B). She succeeded in keeping four of her five young alive through day 60, by which time the fledglings were foraging for most of their own food. In both cases of single parents, the rate per young was less than it had been when both parents were feeding.

Two females whose mates disappeared prior to fledging lost their young within 5 days. In at least one of these cases the failure was partly caused by encroachment on the female's nesting area by a neighboring pair, forcing her to spend much time chasing the intruders.

Care of unrelated young. In 1979 the FR male disappeared during incubation. The female continued incubating but spent 71% of the time she was observed in the nest instead of the 90% typical of other females. A week after her mate was last seen, she began joining a male when she was off the nest, occasionally taking part in courtship. This male was not seen feeding the female, but after another 10 days, when the eggs had hatched, he began bringing her food. Gradually he also began feeding the nestlings. During the first half of the nestling period the female made 76% of the feeding trips (population $\bar{x}$ = 45%). Her rate (3.2 trips/hr) was above average, especially for the first week after hatching, while her new mate's was unusually low (1.0/hr). This male's rate in-

creased to 1.4/hr over the next 3 weeks, while the female's decreased to 1.6/hr. Despite below average feeding rates this pair fledged two of four young.

The reciprocal situation occurred in 1978 when the GO female vanished the day after their six young fledged. Five days later a new female seen near the GO family was courted by the male during breaks between feeding his young. For the next 2 days the female watched the male care for his young, and on the third day she too began feeding them. She fed the young six times in 90 min, and over the next 8 days her rate was 3.8 trips/hr, 42% of total trips. At least five young were still alive 1 week later.

Antipredator behavior. The response of magpies to different types of natural predators is examined in detail elsewhere (Buitron 1983b). I am including here a brief summary only of the differences between males and females.

Mates usually cooperated in driving away dangerous predators by alternately diving closely at the predator and causing it to turn repeatedly to face the mobbing magpies. The female and male were most likely to respond with approximately equal intensity to potential predators (75 of 110 occasions, 68%). However, when one of the pair reacted more vigorously (longer or at a higher response level) it was likely to be the male (33 occasions) rather than the female (two occasions, $P < 0.001$, Sign test).

During laying and incubation females rarely left the nest to attack a predator unless it was very close. As a result, during laying, incubation and brooding of young nestlings, usually only one parent was present and responding to raptors, American Crows (*Corvus brachyrhynchos*), or coyotes (*Canis latrans*), and it was usually the male (57 of 71 instances). When alone, females

attacked red squirrels (*Tamiasciurus hudsonicus*) vigorously, but never responded to raptors by diving at them, as did lone males.

DISCUSSION

VARIABILITY AMONG MAGPIE POPULATIONS

The Wind Cave, South Dakota population of Black-billed Magpies is located near the eastern periphery of their range in North America. This population was less dense (1.9 to 2.5 pairs/km^2) than populations studied in Montana (21.4 pairs/km^2, Brown 1957), Britain (3.5 to 3.7 pairs/km^2, Vines 1981 and 5.0 pairs/km^2, Clarkson 1984; 19 to 26 pairs/km^2, Birkhead et al. 1986), Sweden (6.3 pairs/km^2, Högstedt 1981a), or the Netherlands (7.8 pairs/km^2, Baeyens 1981a). Nests were further apart than those studied by Birkhead (1979) in Britain, and the area defended around a nest was almost half the size of that reported by Baeyens (1981a) or Vines (1981).

In magpies, territoriality is reported as variable, from no nest-associated territoriality in Wyoming (Erpino 1968a) to reasonably well-defined territories in the Netherlands (Baeyens 1981a) and Britain (Vines 1981). At Wind Cave, territories were not clearly defined and, except for a small area around the nest, were closer to dominions in which intruders are dominated but not necessarily evicted (Brown 1975). Except when incubating or brooding, breeding magpies foraged outside of their territories, and used communal roosts. They left their nesting areas altogether for 2 months after fledging young. In Europe (Birkhead 1979, Baeyens 1981a, Högstedt 1981b, Vines 1981, Clarkson 1984, Birkhead et al. 1986), magpies occupy their territories year-round, rarely leaving them, and only non-breeders used communal roosts.

The larger home ranges, lower population density, and lower levels of aggression in my study were associated with several aspects of magpie nesting behavior. Pairs often moved their nest sites considerable distances from one year to the next, which is not typical in other populations. In most cases there were no obvious differences in quality between successive nests, and there did not seem to be any correlation between breeding success and distance moved. Baeyens (1981b) found that although pairs in the best territories were not more likely to move after a breeding failure than a success, those in poorer territories were.

There also appear to be geographical differences in magpie nest construction. Domeless nests have been described regularly in Europe (Raspail 1908, Goodwin 1976, Baeyens 1981c), and occasionally in North America (Linsdale 1937, Jones 1960). In the Netherlands, Baeyens (1981c) showed that domes decreased predation by Carrion Crows (*C. corone*), a major egg and nestling predator. Nest building by magpies in the Netherlands was sometimes severely disrupted by Carrion Crows, possibly preventing the construction of domes (Baeyens 1981c). At Wind Cave, magpies building nests were rarely interfered with by any species and all had domes.

In my study, only one pair split up between one year and the next (8% of 12 pair-years) and only two of 56 pairs (4%) split up within a breeding season, both during nest building. The rate of mate switching was much higher in Baeyens' study (33% in 33 pair-years, 1981b). At Wind Cave, nonbreeding birds were more rarely seen and rapid replacement of dead mates appeared to be less common than has been reported in Europe (Shannon 1958, Birkhead 1979, Baeyens 1981b).

On rare occasions, flocks of nonbreeding magpies moved through my study area but were presumably travelling long distances. This contrasts with the situation in Europe in which nonbreeding flocks are usually in between territories of breeding pairs or around the periphery (Baeyens 1981b, Birkhead et al. 1986). If new potential mates are not readily available, pair bonds may be more likely to last from one year to the next.

PARENTAL CARE

Clutch sizes and incubation and nestling period lengths were similar to those previously reported in North America (Linsdale 1937, Evendon 1947, Brown 1957, Jones 1960, Erpino 1968a) and in Europe (Holyoak 1967; Goodwin 1976; Baeyens 1979, 1981a, 1981b; Birkhead 1979; Vines 1981). At Wind Cave, males generally contributed more to the construction of the nest than females, as was also true in Erpino's (1968a) study and in Verbeek's (1972) study of Yellow-billed Magpies (*P. nuttalli*). There was also a division of labor in nest building, with females bringing a greater proportion of nest-cup lining material and doing more work inside the nest, while males concentrated on the dome and base. However, there was a good deal of variation between individual

pairs, and in several cases these differences persisted from one year to the next.

The two cases of nest building by newly formed pairs are of interest because in both, the bird initiating pair formation immediately began taking part in the construction of a nest, perhaps demonstrating his or her qualities as a mate. Similarly, the high mate-feeding rates of new pairs may have included an element of courtship important to bond-strengthening.

Yearling females laid significantly smaller clutches than older females and tended to fledge fewer young, as was true in Clarkson's study (1984) in Britain and in a variety of other species (e.g., Coulson and White 1958, Klomp 1970, Woolfenden 1974, Harvey et al. 1979, DeSteven 1980). The smaller clutch sizes of yearlings may be an adjustment to less efficient parental behavior or to poorer quality nest areas. In his experimental study of Black-billed Magpies, Högstedt (1980) showed that a particular clutch size is optimal for the pair that lays it, and may vary from pair to pair depending on, for example, territory quality.

As in Yellow-billed Magpies (Verbeek 1972), males appeared to provide mates with almost all their food during laying and incubation. Females had a very high rate of nest attendance (90 to 95%), greater than the rate of 84% recorded by Erpino (1968a), but similar to the 92% found by Verbeek (1972) in Yellow-billed Magpies.

Magpies carry food in a throat pouch, and as it would be most efficient to completely fill the pouch before flying to the nest, the variation in size and weight of each load was probably less than in species that carry a single prey item each trip, such as Great Tits (*Parus major,* Kluyver 1950, Royama 1966) or Black-capped Chickadees (*P. atricapillus,* Kluyver 1961). In the case of magpies, feeding rates may therefore give a better estimate of amounts of food brought, though the quality of the items may still vary.

Adults did not bring food to their offspring at the maximum rate possible. In two cases, parents with fledged young immediately increased their feeding rate after losing their mate. Although each brood lost one young, the rest were raised to independence. In all cases birds losing a mate before the young fledged failed to raise any young unless a new mate was obtained and assisted.

Due to the logistics involved, most passerine studies have not followed young past fledging (but see Morehouse and Brewer 1968, Morton

et al. 1972, Balda and Balda 1978, Smith 1978, Harper 1985). Yet, for magpies, this was a critical period during which both feeding rates by parents and predation on young peaked (Buitron 1983b). Therefore estimates based on nesting success alone are not good indicators of reproductive success. Magpies that have just fledged remain completely dependent on their parents for food, but are more active and no longer benefit from the protection of the nest or the warmth of siblings. Only after 2 weeks are fledged young able to fly reasonably well and find some of their own food, and this food is supplemented by their parents until at least 4 weeks after fledging.

Care of unrelated young. At Wind Cave, two birds cared for young that were not their own, each after having paired with the surviving parent. In neither case did the new bird immediately begin feeding the young. Instead, the first few days were spent courting and watching the single parent care for the young. During this period the two foster parents may have undergone an accelerated physiological adjustment, resulting in the appropriate hormonal conditions for providing parental care, as Emlen (1976) suggests would be necessary. This seems more likely than Power's (1975) suggestion that the new magpies would have to be at the same stage as the birds they joined.

Similar incidents, in which a new mate helps care for young that are not its own, have been reported in several other species: two male Black-capped Chickadees (Odum 1941, Howitz 1986), a male Mountain Bluebird (*Sialia currucoides,* Power 1975); a male Yellow-bellied Sapsucker (*Sphyrapicus varius,* Kilham 1977); a male Purple Martin (*Progne subis,* Brown 1983); and a female Eastern Bluebird (*Sialia sialis,* Hamilton 1943). There are clear advantages to an individual in caring for young of a new mate if (1) potential mates are in short supply or (2) good territories are hard to obtain. The first may have been true in my study, though I lacked the information necessary to verify this.

CONCLUSIONS

In the Black-billed Magpies I studied, males and females cooperated extensively throughout the breeding season in nest building, defense of nest site, care of eggs, feeding of nestlings and fledglings, and defense of offspring from potential predators (Table 7). Yet there was also considerable variation between pairs. Of the types of

TABLE 7.   Summary of the roles of females and males in raising offspring.

	Females	Males
Nest building	Fewer trips About equal time Carried more grass Concentrated on nest cup	More trips About equal time Carried more mud and twigs Concentrated on dome and frame
Care of eggs (25 days)	Laid about 6 eggs Performed all incubation (90–95% of hours) Failed without a mate	Remained close to mate during laying Provided most of female's food Most active against predators Failed without a mate
Care of nestlings (27 days)	Performed all brooding (50% of hours day 1–6) Feeding rate increased to 40–45% of to- tal Likely to fail without a mate	Responsible for 55–60% feeding trips Most active against predators Likely to fail without a mate
Care of fledglings (4–6 weeks)	40–50% of feeding trips Equally active against predators If mate was lost, could raise at least some young	50–60% of feeding trips Equally active against predators If mate was lost, could raise at least some young

parental care that I was able to measure, males contributed more to raising young than females. Males were also more active in expelling intruders, especially during their mate's fertile period, and males took the initiative in driving away predators (Buitron 1983a).

Females spent 30 days almost constantly in their nests incubating eggs and brooding nestlings. However, Mugaas and King (1981) estimated that for magpies the energetic cost of incubating was low compared to that of mate feeding, and from my study and others (Högstedt 1981a) it seems likely that male magpies spend as much if not more time and energy than females in raising offspring.

The repercussions of individually variable degrees of division of labor between mates are many and deserve further study. Incubation systems that involve well developed division of labor between mates can be costly to an individual, since birds that lose their mates are much less likely to be able to take over the specialized role of the other. Magpie males never incubated eggs or brooded nestlings, and are unlikely to be able to raise any young if the female dies much before the young fledge.

The time and energy saved by specialization and division of labor between mates in birds is thus gained only at the expense of a greater risk of total nest failure. This cost of specialization would be high especially for short-lived species or populations of long-lived species that are subject to high predation rates.

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