INFLUENCE OF HIGH DENSITY AND PARENTAL AGE ON THE HABITAT SELECTION AND REPRODUCTION OF BLACK-BILLED MAGPIES

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ABSTRACT.—The habitats selected for nesting and the breeding biology of a dense population of Black-billed Magpies (*Pica pica hudsonia*) were studied over two years in northern Utah. Breeding density was at least twice that previously reported and first-year birds comprised approximately 40% of the breeding population. Nest territories were densely packed in all available habitats and had a mean size of 0.5 ha. Date of clutch initiation was negatively correlated with clutch size and number of fledglings. Earlier nests were more successful than later ones. First-year birds most often occupied marginal habitats and bred less successfully than older adults. Mixed-age pairs were intermediate in reproductive variables. Neither the timing, clutch size, nor success of the reproductive effort were affected by the high density or the large proportion of breeding first-year birds. Females sometimes had lower success, however, if they mated with inexperienced first-year males. Our results suggest that these magpies have a malleable territorial system in relation to density and that high density itself does not limit their production.

Habitat use, territorial behavior, and reproductive performance of a species may depend on food supply, cover conditions, and population density (Lack 1966, Tatner 1982b). For example, the clutch size of passerines may vary inversely with population density (Perrins 1965, Klomp 1970, Krebs 1970) or may be directly related to breeding density, at least in Yellow Warblers (*Dendroica petechia*; Goossen and Sealy 1982). Breeding birds' choice of habitat and their reproductive success also may be strongly influenced by age, adults usually being more productive than immatures (Coulson and White 1960, Harvey et al. 1979, Hannon et al. 1982, Møller 1982).

Black-billed Magpies (*Pica pica hudsonia*) are conspicuous, abundant, permanent residents over much of western North America (Bock and Lepthien 1975). The species is evidently not as highly territorial as some other passerines (Linsdale 1937) and may, under certain conditions, not behave territorially at all (Erpino 1968b). Reported densities of breeding magpies range from 1.8–7.0 birds/40 ha (Jones 1960, Jones and Hungerford 1972, Mugaas and King 1981, Buitron 1983). In Britain, the Magpie (*P. p. pica*) may attain breeding densities of up to 5.6 birds/40 ha (Tatner 1982a), and in Spain, up to 14 birds/40 ha (Alvarez and de Reyna 1974). The influence of local breeding density on territorial behavior, habitat selection, and reproductive performance is unknown. Breeding by first-year

birds, especially males, has rarely been noted in either subspecies (Linsdale 1937; Erpino 1968b, 1969; Baeyens 1981c). We describe here a dense (9.6–13.4 birds/40 ha) population of Black-billed Magpies in which first-year birds comprised 20–47% of the breeding population. We were specifically interested in learning (1) factors that determine the habitat used by breeding magpies; (2) the relationship between high density and territorial defense, territory size, and habitats occupied by the birds; (3) the relationship between high density and day of clutch initiation, clutch size, fledgling number, and nesting success; and (4) the influence of parental age on habitat use and reproductive performance.

STUDY AREA AND METHODS

We conducted our research at two sites in Cache County, Utah, from January 1979 to August 1980. One area (156 ha) was southeast of Millville, where the elevation ranged from 1,400 m on the valley floor to 2,000 m along the western slopes of the Bear River Range of the Wasatch Mountains. The valley floor and low benches comprised pasture, farmland, orchards, and riparian vegetation, which together accounted for approximately half of the study area. The remaining habitats included benches covered with sagebrush (*Artemisia tridentata*), canyons containing big-toothed maple (*Acer grandidentata*), and slopes covered with ju-

niper (*Juniperus osteosperma* and *J. scopulorum*), sagebrush, and talus.

The second area was 26 km north of the first and 0.5 km west of Richmond. It was flat, 1,350–1,390 m in elevation, and encompassed 287 ha of farm and pasture lands, riparian vegetation, and small stands of hawthorn (*Crataegus* spp.) and cottonwood (*Populus* spp.). In both areas, magpies usually nested in small (100 m² or less) stands of trees and linear strips of riparian cover separated by agricultural fields or grassy shrublands.

We captured Black-billed Magpies as adults or immatures in funnel traps (Alsager et al. 1972) and as nestlings. Each captured bird (135 adults and 393 nestlings) received a United States Fish and Wildlife Service aluminum band and three colored plastic bands for individual recognition. All were aged as either adult or first-year (less than one year old) birds using Erpino's (1968a) criteria. The sex of 81 birds was determined either by laparotomy in the field, or during the nesting season, by the presence of brood patches.

We spent 119 h (4–8 pairs were watched simultaneously) watching magpie territorial behavior in February 1979 and January 1980. Active nests were located in late February and were inspected at 3- to 7-day intervals thereafter. Nestlings within 10 days of fledging were inspected every 3–4 days. The age of unbanded birds was frequently determined (in 41% of the birds) while we inspected their nests, because magpies often displayed 1–2 m away, and in these instances the primaries and rectrices were easily classed as those of adult or first-year individuals (Erpino 1968a).

Because magpies are monogamous (Erpino 1968b, Baeyens 1981a), we estimated population density simply by doubling the number of active nests in each area. Both study areas were approximately square in configuration and we located nests only within the 156- and 287-ha areas previously described. Because 18% of the nests at Millville and 19% at Richmond were within 200 m of the boundaries of these study areas, and magpies routinely fly 300–400 m from nests to forage (pers. observ.), some nesting birds were feeding outside the study areas. We added a 200-m wide zone around each study area so that we would have a more realistic and conservative estimate of breeding density. This increased the areas to 250 ha (a 60% increase) and 400 ha (a 39% increase) at Millville and Richmond, respectively. Active nests within this added zone, however, were not examined.

In order to analyze the vegetation, maps of each area were overlaid with a grid of 0.25-ha cell size. Ten percent of the grid intersections (115 at Richmond, 63 at Millville) were then randomly selected to serve as the centers of 0.25-ha (28-m radius) circular plots. A complete list of the 28 vegetational and structural variables measured in these plots and the methods employed to measure them are given in Reese (1982). The variables included tree density, tree basal area, size of tree patch, percent tree canopy cover, percent shrub, grass, and forb cover, distance to water, distance to nearest active and old nest, and distance to nearest two foraging areas (creek bed, pasture, stock yard, row crop). The quality (types and amounts of food available) of foraging areas was not determined. Areas surrounding active nests were analyzed in the same manner except that the nest served as the center of the 0.25-ha circular plot. To compare nest and non-nest sites, only plots with trees suitable for nesting but without nests were used in the analysis. All distance measurements were recorded from either the nest tree or a tree suitable for nesting. An index of vegetation cover surrounding each nest was derived by summing the percent of the nest visible from five paces along the cardinal directions. Percent nest visibility could range from 0 to 400.

Data from sites that did not contain nests were used to determine the types of habitats available to magpies for nesting. Hierarchical cluster analyses (Marshall and Romesburg 1977) using average Euclidean distance produced habitat clusters of plots with similar compositions. Vegetation characteristics of each active nest site were compared with those in each habitat cluster and the nest site was assigned to the habitat cluster it most closely resembled. Distribution of nests among habitats was analyzed by Chi-square, and 95% confidence intervals (CI) were established with Bonferoni-z statistics (Roscoe and Byars 1971, Neu et al. 1974).

To determine the characteristics of the habitats that may have been important to magpies when they selected breeding sites, we used stepwise Discriminant Function Analysis (DFA) of nest and non-nest sites (Cooley and Lohnes 1971, Klecka 1975). The DFA produced a linear equation which maximized and distinguished the discriminating variables (Cooley and Lohnes 1971, James 1971).

Means for dates of first egg and hatching, clutch size, number of young that hatched, and number of young that fledged were compared between years and areas by *t*-tests (Steele and Torrie 1960). Areas and/or years that were not different were pooled. Each of the above reproductive variables was tested, using analysis of variance, for differences between habitat types. Differences in reproductive success of

TABLE 1. Types of habitat available to breeding Black-billed Magpies on two areas in northern Utah.

Study area	Habitat	Mnemonic	Proportion of available breeding habitat	Distinguishing characteristics
Millville	Shelterbelt, riparian, orchard	SRO	0.33	Boxelder (*Acer negundo*), chokecherry (*Prunus virginiana*), willow (*Salix* spp.) patches, and small fruit orchards interspersed with agricultural fields, 1,400–1,465 m elevation
	Juniper-maple-sagebrush bench	JMS	0.17	Junipers and big-toothed maple patches distributed among sagebrush, 1,450–1,525 m elevation
	Low elevation juniper sagebrush slopes	LJS	0.29	Junipers and sagebrush, 15–20% slopes, 30% bare ground and/or rocks, 1,500–1,615 m elevation
	Middle elevation juniper slopes	MJS	0.18	Junipers, sparse sagebrush (<5%), 20–50% slopes, 35–50% bare ground and/or rocks, talus, 1,600+ m elevation
	Mountain mahogany	MM	0.03	Mountain mahogany (*Cercocarpus ledifolius*), north-facing aspect, 50–60% slopes, 1,650+ m elevation
Richmond	Monospecific hawthorn stands	MHS	0.61	Mean tree density (MTD) = 5.0, tree height (TH) = 4.9 m, <2% canopy cover (CC), <7% shrub cover (SC)
	Small, mixed canopy stands	SMC	0.20	Hawthorn, cottonwood, willow, boxelder, MTD = 5.0, TH = 4.6 m, 2–4% CC, 12–20% SC
	Large, mixed canopy stands	LMC	0.09	Cottonwood, boxelder, hawthorn, MTD = 13.0, TH = 6.1 m, 8–15% CC, 14–22% SC
	Mature, mixed canopy stands	MMC	0.07	Cottonwood, boxelder, MTD = 19.0, TH = 9.5 m, 25–35% CC, 7–12% SC
	Livestock-influenced stands	LS	0.03	Cottonwood, hawthorn, MTD = 9.0, TH = 10.4 m, 10–16% CC, <5% SC

birds of different age within habitats, and of similarly-aged birds between habitats, were evaluated by *t*-tests. We excluded nests near bait stations from this analysis because supplemental feeding influences the reproductive success of magpies (Reese and Kadlec 1984). Data are presented as means ± SD. All nonparametric tests follow Hollander and Wolfe (1973).

RESULTS

TERRITORIAL ESTABLISHMENT, TERRITORY SIZE, AND POPULATION DENSITY

Magpies began to establish territories at the end of January by perching alone or in pairs at the highest point in a tree. Other forms of territorial defense were seldom seen. Magpies that foraged further than 35–45 m from active nest sites provoked no response from nest owners. In general, neighboring pairs did not forage near other nests. On only 22 occasions, intruding birds approached closer than 30 m to nests while owners were present. On 12 (54%) of these occasions, the owners attacked and chased the intruder from the immediate area. Territory owners always stopped chasing when the intruder was 50–60 m, and the owner 40–50 m, from the nest, which probably marked the boundaries of territories.

In 1979, individual courtship behaviors, strutting, wing-flirting, and short chases were first seen on 8 February (Millville) and 16 February (Richmond). In 1980, courtship behavior was seen on 23 January at Millville and 19 January at Richmond. Although the earliest

nest-building began during the first week of February (irrespective of year or area), most of it was started during the last week of February or early March.

We found 191 nests and 9 re-nests on both areas over both years. The mean population density was 11.7 ± 1.73 birds/40 ha (range of 9.6–13.4). This density was high compared to those reported in previous studies (discussed below), even though only 12% (19 ha) of the total area at Millville and 9% (25 ha) of that at Richmond provided wooded cover suitable for nesting.

Magpie nests were well-spaced throughout the limited available habitat. Since distances between nests did not differ between years on either area, we combined data for years. The mean inter-nest distance on both areas exceeded the mean distance to the next possible nest site (80 ± 4.8 vs. 14 ± 1.6 m, n = 75, $P < 0.001$, Millville; 61 ± 6.3 vs. 25 ± 3.4 m, n = 124, $P < 0.001$, Richmond).

BREEDING HABITATS: AVAILABILITY AND USE

Hierarchical cluster analysis indicated that five types of habitat were available on each study area (Table 1). Their distinguishing characteristics at Millville were elevation, canopy trees, tree patch size, slope, and percent bare ground and/or rock. At Richmond, canopy species, tree height, tree patch size, and percent canopy and shrub cover determined habitat clusters.

On both study areas, magpies used habitat types differently than expected based on proportion available (χ^2 = 57.84, df = 4, $P <$

TABLE 2. Variables distinguishing nest and non-nest sites at two study areas in northern Utah.

Study area	Distinguishing variable	Sites with nests[a]		Sites without nests[a]
Millville	% cover	16.6	***	10.1
	Distance to winter roost (m)	1,050.1	***	817.7
Rich-mond	% cover	18.2	***	11.3
	Tree patch size (m²)	87.4	***	45.1
	Number of old nests in patch	2.0	***	0.6
	Distance to nearest active nest (m)	41.1	***	20.9
	Distance to nearest old nest (m)	8.8	**	13.2

[a] Values in these columns are means. Pairs differ at the 0.012 (**) or 0.001 (***) level of significance (2-tailed t-tests; data were transformed to square root or natural logarithm equivalents for analysis).

0.005, Millville; $\chi^2 = 32.87$, df = 4, $P < 0.005$, Richmond). They nested in shelterbelt-riparian-orchard habitat more than expected at Millville (proportion of area = 0.33, proportion of observations = 0.71, 95% CI = 0.57–0.84), and used juniper slopes less than expected (at lower elevations [LJS in Table 1]: proportion of area = 0.29, proportion of observations = 0.07, 95% CI = 0.00–0.14; at middle elevations [MJS in Table 1]: proportion of area = 0.18, proportion of observations = 0.03, 95% CI = 0.00–0.08). None of the habitats at Richmond were used more than expected, but monospecific hawthorn stands were selected for nesting less frequently than expected (proportion of area = 0.61, proportion of observations = 0.39, 95% CI = 0.21–0.57).

Discriminant Function Analysis revealed the distinguishing characteristics of nest and non-nest sites on each area, and correctly classified 73.3% of the Millville cases and 83.5% of the Richmond cases. For the Millville nests, DFA used two variables, the square root of the total percent woody cover (TTWC), and the natural logarithm of distance to the winter roost. Nest sites were farther from the roost and had more woody cover than non-nest sites (Table 2). The means for these variables, plus several related to woody cover, in the habitats at Millville suggested that TTWC was a key feature in the location of magpie nests (Table 3). Five variables distinguished nest from non-nest sites at Richmond: TTWC, the natural logarithm of tree patch size, the number of old nests in the patch, distance to the nearest active nest, and distance to the nearest old nest. Nest sites had denser cover and larger patches than non-nest sites (Table 2). Areas that were under-used by nesting magpies tended to offer less total and canopy cover, and smaller patches of trees than other areas used by the birds (Table 3). Preference for particular tree species was not important in selecting a nest site, since the species were used in proportion to their overall availability ($\chi^2 = 10.494$, df = 8, $P > 0.10$). Habitats did not differ in distance to the nearest or to the second closest foraging area. Mean distance to the second nearest foraging area tended to be greater, however, for the under-used habitats (93.5 ± 77.9 m) than for equally- (63.5 ± 7.8 m) and over-used (36 m) habitats.

REPRODUCTIVE BIOLOGY

The chronology of nesting did not differ between years or study areas. For the population as a whole, mean date of the first egg ($n = 172$) was 14 April (range: 26 March–16 May), mean hatch date ($n = 150$) was 8 May (range: 4 April–6 June), and mean fledging date ($n = 66$) was 31 May (range: 11 May–13 June). Differences related to the ages of birds are presented below.

Clutch size varied from 1–9 eggs with a mean of 6.5 ± 1.1 eggs (Table 4). Differences in mean clutch size and number of young fledged between years and between areas were not significant ($P > 0.10$ in all cases). At Millville, there was one clutch of 1, nine clutches of 5,

TABLE 3. Some characteristics of patches of trees in the habitats available to Black-billed Magpies for breeding. Values in the table are means ± SD.

Study area	Habitat[a]	Use category[b]	Characteristic of patch		
			% total cover	% canopy cover	Patch size (m²)
Millville	SRO	M	11.6 ± 9.4	7.9 ± 7.2	79 ± 78
	JMS	E	14.6 ± 12.7	11.8 ± 12.2	44 ± 29
	LJS	L	9.6 ± 8.6	6.8 ± 8.4	33 ± 16
	MJS	L	11.8 ± 6.7	5.7 ± 3.3	27 ± 13
	MM	E	10.8 ± 2.6	7.0 ± 1.7	18 ± 4
Richmond	MHS	L	7.9 ± 8.4	1.7 ± 1.9	52 ± 48
	SMC	E	19.3 ± 10.4	3.2 ± 3.2	89 ± 88
	LMC	E	25.6 ± 14.0	9.7 ± 5.9	88 ± 79
	MMC	E	36.9 ± 17.4	26.2 ± 13.6	112 ± 50
	LS	E	17.8 ± 16.4	13.5 ± 11.7	111 ± 94

[a] See Table 1 for definitions of these mnemonics.
[b] Letters indicate that the habitat was used more than expected (M), used in proportion to availability (E), or used less than expected (L).

TABLE 4. Nesting data for Black-billed Magpies from two areas in northern Utah.

	Millville	Richmond	Both areas
Number of nests	68	116	184
Number of eggs	447	745	1,192
Clutch size[a]	6.6 ± 1.2	6.4 ± 1.1	6.5 ± 1.1
Number of young hatched per nest[a]	4.5 ± 2.4	3.4 ± 2.6	3.8 ± 2.6
Number fledged	180	236	416
Number of young fledged per nest[a]	2.6 ± 2.4	2.0 ± 2.3	2.2 ± 2.4
% successful nests	67.6	50.0	56.5
Number of young fledged per successful nest[a]	3.9 ± 1.9	4.1 ± 1.5	4.0 ± 1.6

[a] Values in the table are means ± SD.

19 of 6, 27 of 7, 10 of 8, and two of 9 eggs. Forty-eight eggs were depredated, 11 abandoned, 44 infertile, and 307 hatched (we were unsure of the fate of 37). Thirty nestlings were depredated, 90 died in the nest, and 180 fledged. At Richmond, there was one clutch of 3, five of 4, 14 of 5, 38 of 6, 40 of 7, 16 of 8, and two of 9 eggs. One hundred-forty-one eggs were depredated, 19 abandoned, 71 infertile, and 398 hatched. Seventy-five young were depredated, 73 died in the nest, and 236 fledged. On both areas, clutches of seven and eight eggs were most productive with over 65% fledging at least one young. Date of clutch initiation (excluding re-nests) was negatively correlated with clutch size, number of young hatched, and number of young fledged (Millville [$n = 65$]: $r = -0.447$ [$P < 0.001$], -0.387 [$P < 0.001$], and -0.413 [$P < 0.001$], respectively; Richmond [$n = 77$]: $r = -0.502$ [$P < 0.001$], -0.255 [$P < 0.025$], and -0.237 [$P < 0.038$], respectively).

Over both years of the study we found nine cases of re-nesting (approximately 10% of destroyed nests). All followed losses of eggs and took place in the original nest. No females re-nested after losing their nestlings. The maximum length of time between loss of eggs and the initial egg of the replacement clutch averaged 16 ± 5.1 days (range 12–27 days). Re-nests had fewer eggs (5.8 ± 1.3) and fledglings (1.6 ± 2.0) than the initial nests, but the differences were not statistically significant.

At three of four nests from which a parent was lost, the bird was replaced within three days. In one nest, the replacement bird removed the original clutch of five eggs and laid another one. Flocks (5+ birds) were not seen until mid- to late-April, after nesting attempts of numerous pairs had failed.

EFFECTS OF HABITAT ON REPRODUCTIVE VARIABLES

At Millville, magpies laid eggs earlier in heavily-used habitat (shelterbelt-riparian-orchard) than in the others (Table 5). At Richmond, the under-used habitat (monospecific hawthorn stands) was characterized by low hatching success and number of young fledged. Nest success was greater in preferred (heavily- and equally-used) than in under-used habitats (Binomial test, 0.69 vs. 0.57, $P = 0.022$, at Millville; 0.55 vs. 0.38, $P = 0.001$, at Richmond).

Predators destroyed 25% of the nests at Millville and 33% of those at Richmond. These rates were not significantly different ($B^* = -1.452$, $P = 0.147$, Binomial test, large sample approximation). Weasels (*Mustela* spp.) and American Crows (*Corvus brachyrhynchos*) were the primary predators of both eggs and young.

TABLE 5. Relationships between habitat types and reproductive performance of Black-billed Magpies.

Study area	Habitat[a]	Use class[b]	Number of nests	Date of first egg[c,d]	Number of eggs hatched[c]	Number of young fledged[c]
Millville	SRO	M	53	101 ± 6.9 a	4.8 ± 2.3 a	2.6 ± 2.4 a
	JMS	E	15	110 ± 10.3 b	4.3 ± 2.5 a	2.8 ± 2.3 a
	LJS	L	5	115 ± 2.8 b	3.8 ± 1.9 a	1.4 ± 1.5 a
	MJS	L	2	107 ± 8.5 ab	—	1.0 ± 1.4 a
Richmond	MHS	L	48	105 ± 7.0 a	2.9 ± 2.7 b[c]	1.7 ± 2.5 a
	SMC	E	31	104 ± 5.7 a	3.1 ± 2.7 b	1.6 ± 2.2 a
	LMC	E	18	105 ± 4.8 a	4.5 ± 2.5 a	2.3 ± 2.2 a
	MMC	E	18	105 ± 6.5 a	3.8 ± 1.8 ab	2.7 ± 2.1 a
	LS	E	9	103 ± 5.8 a	5.1 ± 2.2 a	2.9 ± 2.4 a

[a] See Table 1 for definitions of these mnemonics.
[b] See Table 3 for definitions of these use classes.
[c] Means ± SD: values in each column, for each study area, are not significantly different ($P > 0.05$) if followed by the same letter; values followed by different letters differ at the 0.001 level (Analysis of Variance and Least Significant Difference tests), except for superscript [e].
[d] Julian date.
[e] Significantly different at $0.10 > P > 0.05$ (Analysis of Variance) and $P < 0.05$ (Least Significant Difference test).

TABLE 6. Reproductive performance of adult, first-year, and mixed pairs of Black-billed Magpies. Values in the table are means ± SD.

Age class[a]	Number of nests	Date of first egg[b,c]	Clutch size[b]	Number of eggs that hatched[b]	Number of young fledged[b]	Number fledged per nest containing chicks[b]	Number fledged per successful nest[b]	% nests success-ful[d]
2Y	10–20	105.4 ± 5.8 b	6.2 ± 1.0 a	4.5 ± 2.0 a	1.9 ± 2.3 a	2.0 ± 2.3 a	3.9 ± 1.5 a	50 b
YM, AF	5–9	103.5 ± 6.5 ab	6.4 ± 1.0 a	4.7 ± 1.7 a	2.2 ± 2.3 a	2.2 ± 2.3 a	4.0 ± 1.2 a	56 b
AM, YF	6–7	106.8 ± 4.9 b	6.6 ± 1.0 a	4.8 ± 2.1 a	3.6 ± 2.4 a	3.6 ± 2.4 a	4.2 ± 1.9 a	86 a
2A	26–33	100.3 ± 7.1 a	6.9 ± 0.9 a	5.3 ± 2.0 a	3.3 ± 2.1 a	3.6 ± 2.0 a	4.1 ± 1.5 a	82 a

[a] A—adult, Y—first-year, M—male, F—female.
[b] Values followed by the same letter are not significantly different ($P > 0.05$); values followed by different letters differ significantly at the 0.05 level (Analysis of Variance and Least Significant Difference tests).
[c] Julian date.
[d] Values followed by different letters differ significantly at the 0.05 level (Binomial test).

We observed both animals entering magpie nests and found several broods killed by bites to the head and neck. There were no differences in the vulnerability of nests due to habitat types (Millville: $\chi^2 = 0.411$, df = 3, $P > 0.90$; Richmond: $\chi^2 = 8.296$, df = 4, $P > 0.05$). In fact, nest visibility did not differ between habitat types. Pooling data from four equally-used habitats at Richmond, however, gave a predation rate that was lower (18/76) than that in the under-used habitat (23/47, $P < 0.001$).

EFFECTS OF AGE ON REPRODUCTIVE VARIABLES

A large percentage of the breeding population on both areas consisted of first-year birds. Over both years of the study, first-year females comprised 40% of 94 known-age breeding females, while first-year males comprised 47% of 94 known-age breeding males. Mixed-age pairs comprised 21.3% (16/70) of known-age breeding pairs. Age classes differed overall in their choice of habitats ($\chi^2 = 9.04$, df = 4, $P = 0.063$). Adult pairs nested significantly more often in over- or equally-used (15 and 20 nests, respectively) habitats than in under-used (3 nests) ones ($\chi^2 = 36.45$, df = 2, $P < 0.005$), whereas first-year and mixed pairs nested more frequently in equally- and under-used (23 and 9 nests, respectively) habitats than in over-used (5 nests) ones ($\chi^2 = 22.39$, df = 2, $P < 0.005$). Nest site fidelity was difficult to determine because birds may have disappeared from the areas owing to either movement or death. To examine fidelity, we used data from marked birds that nested both years. Four (two first-year males, one adult male, and one first-year female) of seven birds changed territories. In three cases, the fates of the previous partners were unknown, but in one case a pair bond dissolved and the adult male changed territories while the first-year female remained. Each bird fledged young the next year. The birds also fledged offspring before the change in three of four cases. One pair of adults remained on territory both years.

Adult pairs started laying earlier, were more successful, tended to have larger clutches and to fledge more young than first-year pairs (Table 6). The values of the reproductive variables for mixed pairs were generally between those for adult and first-year pairs.

To eliminate possible influences of differential habitat use on the reproductive variables of the different age classes, we compared the reproductive performance of adults ($n = 20$) and first-year ($n = 12$) breeders in the equally-used habitats; there were too few data to include the mixed pairs. Adults were more successful at fledging young (15/20 nests) than were first-year pairs (7/12 nests; Binomial test, $P = 0.065$), but other reproductive variables were not different between age classes.

Differences in parental age were eliminated as a possible confounding variable by comparing, for adult pairs, reproduction in the over- and equally-used habitats and, for first-year pairs, reproduction in equally- and under-used habitats. For adults, pairs nesting in the equally-used habitats had lower percent nest success (15/20 nests) than pairs nesting in over-used ones (14/15 nests; Binomial test, $P = 0.0505$). Among first-year pairs, those nesting in under-utilized habitats had lower percent nest success (2/6 nests) than pairs in equally-used habitats (7/12 nests; Binomial test, $P = 0.0329$). In short, the birds' reproductive success differed between habitats.

DISCUSSION

TERRITORIALITY

Magpies in western Europe are territorial throughout the year and prefer small copses rather than large woods for nesting (Holyoak 1974, Högstedt 1980). Their nests are widely spaced, 82–158 m (Holyoak 1974, Birkhead 1979), their territories large, 5–6 ha (Vines 1981, Møller 1982), and they behave territorially by sitting, chasing, and fighting (Baeyens 1981c). These magpies forage within their territories, often within 100 m of the nest (Högstedt 1980). Buitron (1983) reported that Black-billed Magpies space their nests at 300-m

intervals and have territories of 3.1 ha, in contrast to Erpino's (1968b) finding that they showed little territorial behavior and occasionally nested within 40 m of one another. We found that territorial encounters were low, 0.1/h, compared to 1.2/h reported by Birkhead (1979). Given a mean inter-nest distance of 80 m, the 40- to 50-m radius of intolerance mentioned previously, the high population densities of breeding birds on both of our study areas (9.6–13.4 birds/40 ha), and the assumption that territories were circular (Møller 1982), then the effective territory size in our study (0.5 ha) was extremely small. Indeed, some nests were only 10 m apart, although these tended to be visually isolated from one another by dense vegetation.

Our observations suggest that Black-billed Magpies defended a small area immediately around the nest, and tended to avoid the nests of conspecifics passively, through advertisement, rather than actively, by displays or encounters. Territories were rarely used for foraging, which may account for their small size. Sitting in tree-tops, the magpies' territorial behavior appears to be energetically inexpensive, highly conspicuous, and effective in spacing nests throughout the available habitat.

We saw nothing that indicated any magpies were excluded from breeding despite their high density on the study areas. In fact, large numbers of first-year birds nested in contrast with studies by Erpino (1968b), Holyoak (1974), Baeyens (1981c), and Buitron (1983). If any birds were excluded from breeding they must have vacated the areas or died.

REPRODUCTION

Our results concerning the timing of reproductive events for magpies are similar to those reported for establishment of territory (Holyoak 1974), nest-building (Erpino 1968b, Mugaas and King 1981), clutch initiation (Erpino 1968b, Buitron 1983), and hatching date (Jones 1960). The date when egg-laying begins is significantly negatively correlated with clutch size and the number of fledglings produced, indicating that earlier clutches are larger and more successful. Later clutches also tend to be smaller in *P. p. pica* (Tatner 1982b) and many other birds (Perrins 1965, Klomp 1970, Middleton 1979).

The timing and size of clutches are undoubtedly the result of a balance between opposing factors. A female should delay egg-laying in order to accumulate sufficient nutritional reserves to lay a large clutch, but earlier fledging may enhance the survival of her chicks (Loman 1982). The latter may be influenced by less food for later broods or increased preda-

tion as the season progresses. The size and timing of clutches depend upon the availability of food before egg-laying, mediated by the individual females' ability to feed. Little food may be available for egg production by magpies, i.e., more than the amount needed for survival. Experimentally provisioned magpies laid eggs earlier than normal (Högstedt 1981a), as did Carrion Crows (*Corvus corone*; Yom-Tov 1974, Loman 1980). Tatner (1982b) found that urban magpies laid eight days earlier than rural magpies, probably owing to supplemental food supplies around human dwellings. On our study areas, clutches were initiated earlier by pairs of magpies that nested closer to bait stations used for observation of banded birds than by pairs nesting farther away (Reese and Kadlec 1984). Since the eggs of Black-billed Magpies from northern Utah weigh, on average, 9.41 g (Lee Jones, pers. comm.), and 25 adult females weighed, on average, 163.2 g, a clutch of 6 or 7 eggs is 34.6 or 40.0%, respectively, of the female's body weight. While these are not large percentages of female weight for a clutch (see Perrins 1970), acquiring sufficient nutrition (especially calcium; Turner 1982) to commence early laying may be difficult for female magpies in general, and could have been especially difficult for the dense populations we studied.

Our data, however, fail to support this idea. The date when egg-laying began was similar to that reported in other studies; clutch size was well within the range of values (5.6–7.1 eggs) in the literature (Jones 1960, O'Halloran 1961, Johnson 1972, Buitron 1983), as was percent nest success (50–62%; Dice 1917, Buitron 1983). The mean number of young fledged from all nests (2.2) and from only successful nests (4.0) were slightly lower than most values previously reported (2.4–3.3 and 3.5–4.8 chicks, respectively; Dice 1917, Johnson 1972, Buitron 1983), but this was probably a result of the large proportion of first-year birds in the breeding population (discussed below). In other words, the high breeding density on our areas apparently had no effect on clutch size, number of young fledged, or nest success, which would not likely have been the case if food had been scarce.

EFFECTS OF PARENTAL AGE ON
HABITAT USE AND REPRODUCTION

Although first-year male Black-billed Magpies are physiologically capable of breeding, they generally do not breed (Linsdale 1937, Erpino 1968b, Buitron 1983). In fact, most non-breeding magpies (*P. p. pica, P. nuttalli*) are first-year birds (Verbeek 1972, Holyoak 1974, Baeyens 1981a). In contrast, approximately

40% of the breeding pairs on our areas were first-year birds. Both habitat occupancy and reproductive performance were related to parental age. Adults nested in the better habitat, started laying earlier, and had greater nest success than first-year birds. Differences in reproductive performance between age classes have been reported for several birds (Crawford 1977, Blus and Keahey 1978, Baeyens 1981a). They have not hitherto been evaluated adequately for Black-billed Magpies owing to the paucity of data on breeding first-year birds. Our results for mixed pairs closely agree with those obtained by Harvey et al. (1979) for Great Tits (*Parus major*). Although our small sample sizes preclude statistical comparisons, experience of adult males appeared to have an important influence on nesting success. Both adult and first-year females were similar in reproductive variables and percent nest success when mated with adult males. First-year males, however, appeared to impair the breeding of adult and first-year females, particularly with respect to percent success. We do not know the behavioral or ecological factors producing these results. Adults may be more experienced and efficient foragers (Pugesek 1980, Ross 1980), may invest more in reproductive effort (i.e., risks taken and energy expended; Pugesek 1980), or may be physiologically capable of breeding earlier (Erpino 1969). Breeding experience, particularly with respect to selection of nesting habitat, may be especially important in the breeding success of magpies (Högstedt 1980, 1981a).

Sites with more than average woody cover and larger patches were used for nesting more than expected, and sites with low cover and patch size were used less than expected (Table 3). The results of DFA and cluster analysis suggest that the nesting habitats differed in the degree to which they offered protection from predators. Baeyens (1981a, b) found that territories with more (mean of 59%) tree cover were of better quality for magpies in Europe than more open sites (39%), particularly in relation to predation by Carrion Crows. Tatner (1982a) reported that magpies in England preferred to nest in species of trees that provided a fairly dense, thicket-like canopy, also for protection from crows. Although the cover values of Baeyens' study are considerably greater than those of our study, the relationship is similar: magpies preferred nest sites with sufficient cover (Table 3).

Magpies on our areas nested at high densities on small territories and did not forage exclusively within them, but often flew 300–400 m from their nests to unoccupied, row crop, and pasture lands to feed. Differences in territory quality may nonetheless have been a function of food availability, in the sense that distance between food sources and the nest determined the amount of time parents spent away from the nest and thereby influenced risks of predation. Yom-Tov (1974) reported that Carrion Crows who were given supplemental food had higher than normal reproductive success, which he attributed to better parental protection from predators.

The overall trend for earlier nesting, larger clutches, and more fledged young in habitats of better quality may largely reflect the fact that they were occupied by adult birds. First-year birds were over-represented in the under-used habitats and had lower reproductive success than adults, even though the mean number of young fledged per successful nest (4.1 for adults vs. 3.9 for first-year birds) was similar in the two age classes (Table 6). The low cover and the relatively greater distance to foraging areas of the under-used sites appears to be related to greater predation (perhaps owing to lack of parental attention), which was significantly higher in the under-used habitats than in equally-used habitats in the Richmond area. Although we could detect no differences in nest visibility between habitats, nests in small patches of cover may have been more readily discovered and robbed by crows and weasels than those in larger patches. Nests would also have been more vulnerable if parents spent much time foraging far from the nest (Yom-Tov 1974, Högstedt 1981a, Martindale 1982).

Because the populations of breeding birds were dense in both areas, first-year birds had difficulty securing nest sites in the more desirable habitats, which were occupied by adults. Baeyens (1981a) recognized two types of territory based on proportion of woody cover and proximity to nests of Carrion Crows. Class I territories usually had more cover and were farther from crow nests than class II territories. First-year magpies in her study most often occupied class II sites and moved, when possible, to class I sites for the next breeding season. Although such differences in territory quality existed on our study areas, they were too small to deter breeding by first-year individuals. Perhaps, therefore, especially in risk of predation, most first-year birds shift to better sites for their second breeding attempt, as in the situations described by Baeyens (1981a) and Møller (1982).

Black-billed Magpies in northern Utah were unique in their high breeding density and the large proportion of first-year breeders. A high proportion of first-year breeders might be expected if population density were low and nest-

ing areas were devoid of adults, but our conservative estimates of density were twice those reported in previous studies of this species. The large proportion of first-year breeders was probably a result of the same environmental conditions that gave rise to the dense populations—possibly abundant food and cover. High density apparently did not affect the reproductive biology of the birds. Magpies adjusted to it behaviorally by reducing territory size and avoiding one another's nest sites. They nevertheless acquired sufficient food to produce clutches of normal size and to maintain nesting success. We do not know how breeding density was actually influenced by habitat quality and food supplies, but high density alone did not limit production. In a species with an annual mortality rate of 35–50% (Holyoak 1974, Högstedt 1981b), the capacity to breed successfully in the first year must incease fitness over the individual's lifetime.

ACKNOWLEDGMENTS

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