The Auk 113(1):189-199, 1996

BROOD REDUCTION AND SIBLICIDE IN BLACK-BILLED MAGPIES (*PICA PICA*)

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ABSTRACT.—In many avian species, brood reduction is considered to be adaptive and may be attributed either to sibling competition (passive starvation, active sibling aggression) or parental effects (manipulation of hatching spread, active infanticide). However, nonadaptive factors such as environmental effects, may contribute substantially to nestling mortality. I determined mechanisms of brood reduction and survival probabilities of nestling Black-billed Magpies (*Pica pica*) in relation to intraclutch egg-size variation, brood size, nestling age and size, and weather. Median brood survival time was weakly, but positively, correlated with intraclutch egg-mass variation. Starvation accounted for most nestling mortality within the first 9 days posthatching, although 12 dead and moribund nestlings were found badly bruised around the head. Siblicide and sibling cannibalism were observed in two broods and implicated in the deaths of nestlings in three other broods. Siblicidal events occurred when nestlings were between 15 and 20 days old. Expected median survival times and probability of survival to fledging of nestlings was not linearly related to brood size at hatching, being highest for broods of five, lowest for broods of three, and intermediate for broods of four and six. Dead nestlings were smaller and lighter than surviving siblings at any age; however, asymptotic body mass and linear measurements were negatively correlated with brood size at fledging. The probability of mortality was affected by prevailing weather conditions; rain and low temperatures doubled the estimated risk of death for young nestlings, independent of brood size. These data suggest that factors influencing the occurrence and maintenance of brood-reduction strategies in a population may be more complex than previously thought. Brood-reduction mechanisms are affected by the interaction of biotic and abiotic factors, and may vary in response to factors outside of either parental or offspring control. *Received 9 September 1994, accepted 25 April 1995.*

IN MANY SPECIES of birds, brood reduction can be attributed to starvation of the youngest or weakest nestlings in a brood; this may be regarded as a type of passive sibling competition (Lack 1954, 1968, Ricklefs 1965, Clark and Wilson 1981, Mock 1994). Brood reduction also may result from direct sibling aggression, in which "marginal" young are killed by siblings (Meyburg 1974, Edwards and Collopy 1983, Mock 1985, 1994, Stanback and Koenig 1992). Parental manipulation of hatching spread (hatching asynchrony) may influence both the occurrence and outcome of sibling competition by generating competitively—disadvantaged offspring (Lack 1954, 1968, Mock 1994); additionally, parents may directly manipulate brood size by killing young (Stanback and Koenig 1992).

There are at least three basic assumptions inherent to many models of brood reduction. First, both brood reduction and hatching asynchrony are assumed to be adaptive, inasmuch as the decrease of the brood to a size which can be fed results in the maximization of the number of viable young fledged (Lack 1954, 1968, Howe 1976, Clark and Wilson 1981, Husby 1986, Mock 1994). In particular, hatching asynchrony was interpreted by Lack (1954, 1968) as an adaptive mechanism for producing marginal offspring. Because hatch order determines size differences between siblings, and the relative size differences between young in a brood contribute to competitive outcome, this leads to the second assumption, namely, that mechanisms of brood reduction should be directed towards the smallest and weakest brood members. Finally, food supply is assumed to be the critical factor limiting nestling survival. Sibling competition is expected to increase in importance when there are major discrepancies between food supply and offspring demand. Total offspring demand will increase both with brood size and nestling age; thus, because of the relative increase of potential competitors, nestlings in large broods may be proportionately more restricted in access to food than those in smaller broods.

Because adaptive explanations for brood-reduction mechanisms have received most attention, the effects of nonadaptive factors on brood loss have rarely been considered. However, breeding success and nestling survival for many birds are strongly affected by environmental factors (Murphy 1985). Extremes in temperature and rainfall will significantly impact nesting success of many species of birds by depressing insect availability, therefore affecting the major food source for nestlings and curtailing available foraging time (Lack 1954). Ambient conditions also may affect nestlings directly. When ambient temperatures are low, young nestlings may show thermoregulatory compromise and chilling independent of brood size (Hill and Beaver 1982); very high-temperature and solar-radiation loads also may be implicated in deaths of exposed nestlings (Murphy 1985). Thus, the incidence and timing of brood-reduction mechanisms may be the result of nonadaptive constraints on individuals, rather than purely adaptive responses to current conditions.

In this paper, I present data on patterns and probability of nestling mortality for the Black-billed Magpie (*Pica pica*). Magpie clutch size is unusually large in comparison to most corvids—clutches generally average six to eight eggs, in contrast to the three to five egg clutch characteristic of many corvid species (Goodwin 1986, Birkhead 1991). However, magpies rarely fledge more than two to four young (Högstedt 1981, Goodwin 1986, Buitron 1988, Birkhead 1991). I examined the combined effects of three biological factors (nestling age, brood size, and within-brood nestling-size differences) and several weather variables on the probabilities and distribution of nestling survival over the nesting period. I compared the relative influence of these factors on the incidence of two major types of brood-reduction mechanisms—starvation and siblicide. Starvation has been demonstrated experimentally to be a major factor in magpie nestling mortality (Högstedt 1981, Hochachka and Boag 1987); however, siblicide and sibling cannibalism have not been previously reported for magpies (or, in fact, for any other passerine species). The occurrence of both brood-reduction mechanisms in the same population, and even within a single nest, suggests that factors influencing the both the incidence and the timing of specific brood-reduction mechanisms may be more complex than previously thought. Brood-reduction mechanisms are affected by the interaction of biotic and abiotic factors, and may vary in response to factors outside of either parental or offspring control.

METHODS

I studied breeding Black-billed Magpies in Missoula County, Montana (46°55′N 114°6′W, elevation 973 m), from late March to late June 1994. I measured length and width of 118 eggs in 25 complete clutches to the nearest 0.01 mm with digital calipers. I obtained morphometric data for a total of 110 nestlings from 22 broods every two days from hatch to fledging or death/disappearance. Nestlings were individually marked with nontoxic permanent marker on the underside of the manus and tarsus until old enough to color band. I measured length of head, culmen, manus, and tarsus, to the nearest 0.01 mm with digital calipers; body mass was measured with Pesola scales. Whenever possible, dead young were collected, measured and examined for injuries. When nestlings disappeared between census days, I used data obtained during the last census day young were seen alive in comparisons with surviving young on that day. I obtained daily weather data from the National Weather Service, Missoula; the weather station was within a radius of 2 km of the study sites.

Mortality.—I examined the effects of biotic and abiotic factors on nestling lifetime using survival analysis. The key feature of survival analysis which distinguishes it from other types of statistical analysis is that it handles "censored" data. Censoring occurs when certain individuals cannot be observed for their entire lifetime, and the event of interest (in this case, death) has not occurred within the duration of the study; thus, exact survival times are known only for a certain subset of the study population. Survival distributions and instantaneous probability of death were modelled by survival functions $S(t)$ and the cumulative hazard function $h(t)$; these functions are related to each other by $h(t) = -\log S(t)$ (Lawless 1982).

I used the Kaplan-Meier, or product-limit, survival estimator (Kaplan and Meier 1958) to estimate the cumulative survival probabilities of nestlings from different brood sizes at hatch. The Kaplan-Meier estimator is given as:

$$\hat{S}(t) = \prod_{i=1}^{t} \frac{n_i - d_i}{n_i}, \tag{1}$$

where n_i is the number of nestlings alive at the beginning of a given time interval (specified as t_{i-1} to t_i), and d_i is the number of nestlings that died during that interval. The standard error of $S(t)$ is:

$$\mathrm{SE}[\hat{S}(t)] = S(t)\left[\sum_{i=1}^{t} ((d_i)/[n_i(n_i - d_i)])\right]^{0.5} \tag{2}$$

(Kaplan and Meier 1958, Lawless 1982, White and Garrott 1990). The median survival time is the first observed time when the cumulative survival is 50% or less.

I used pairwise log-rank tests (Lawless 1982) to test the null hypothesis that survival did not differ between sizes of brood at hatching. The test statistic is

$$U = \sum_{i=1}^{t} [d_{obs}(i) - d_{exp}(i)], \quad (3)$$

where $d_{obs}(i)$ and $d_{exp}(i)$ are the observed and expected number of deaths, respectively, at each time interval i. The probability levels were multiplied by the number of comparisons made (Bonferroni's correction) to adjust the significance levels for multiple comparisons (Neter et al. 1985).

I assessed the relative influence of environmental variables on nestling survival times with Cox, or proportional hazards, regression (Cox 1972, Lawless 1982, White and Garrott 1990). The general form of the Cox regression model used was:

$$h(t) = [h_0(t)]e^{(B_1X_1 + B_2X_2 + \ldots + B_pX_p)}, \quad (4)$$

where $h(t)$ is the hazard function, or the instantaneous probability of death at time t, h_0 is the baseline probability of death, B_1 through B_p are the regression coefficients, and X_1 through X_p are the predictor variables. Variables with positive regression coefficients are associated with decreased survival times, whereas variables with negative coefficients are associated with increased survival times. The percentage change in the hazard rate for a unit change in a given predictor variable is calculated as e^B. For binary variables, e^B is the relative risk, or the ratio of the estimated hazard for a case when the factor occurs to that for a case when the factor is absent.

I considered the effects of brood size at hatch and five environmental variables: maximum daily temperature (TMAX, °C), minimum daily temperature (TMIN, °C), total daily sunshine (SUN, min), wind speed (WIND, km/h), and precipitation (PRECIP; no = 0, yes = 1). I fitted separate regression models to data for four nestling ages: day of hatching (day 0), day 5, day 10 (the postulated age of thermoregulatory competence for medium-sized altricial birds; Dunn 1975), and day 20. Predictor variables were selected for inclusion in the model for each nestling age class by backwards selection (Draper and Smith 1981), with the criterion for removal based on the conditional-likelihood estimates of the likelihood-ratio statistic and observed significance level of 0.1 (Norusis 1993). The partial correlation r_p of the estimated death rate with each independent variable was calculated by the relation:

$$r_p = \pm([W - (2\mathrm{df})]/(-2LL))^{0.5}, \quad (5)$$

where W is the Wald statistic (distributed as chi square), df is degrees of freedom for the coefficient, and LL is the log-likelihood for the initial model (Norusis 1993).

I used chi-square tests to assess whether the proportion of young fledged was associated with brood size at hatching.

Morphometrics.—Egg mass is correlated with both hatchling mass and the probability of nestling survival (Howe 1976, Slagsvold et al. 1984, Birkhead 1991). Increased intraclutch variation in egg size may be selected for in magpies and other species characterized by large clutch sizes, hatching asynchrony, and brood reduction (Slagsvold et al. 1984). Unfortunately, it was not possible to obtain precise measurements of hatchling mass for the majority of nestlings, nor could I match each egg with a specific nestling once hatched. I estimated egg mass M_{egg} from the formula $\pi(LW^2)/6$ (where L is egg length and W is egg width), and intraclutch egg-size variation from the coefficient of variation of egg mass (CV = SD/average egg mass) for each brood. I assessed the association of intraclutch egg mass variation (ln CV) with median brood-survival time by the survival function

$$S(t\,|\,X) = S_0(t)^g, \quad (6)$$

where g is e^{BX}, B is the regression coefficient, and X is (ln CV).

I evaluated differences in body mass and four linear variables (head, culmen, manus, and tarsus) between surviving and dead young for three age classes. Age classes were defined as: (age class I) days 0–8 (rapid growth phase); (age class II) days 9–15 (commencement of feather growth and beginning of thermoregulatory competence); and (age class III) days 16–24 (asymptotic growth phase). Morphometric data were analyzed by multivariate ANOVA (linear measurements only) and univariate t-tests. Because the alternative hypothesis of interest is that surviving young are larger than dead young in a given age class, univariate tests were one-tailed. Data were $\log_e$-transformed before analysis to meet normality and homoscedasticity assumptions (Steel and Torrie 1980, Johnson and Wichern 1982). Association between brood size at fledging and asymptotic values of the five morphometric variables were assessed by correlation.

Siblicidal broods were designated as broods for which at least one siblicidal event, defined as the severe physical wounding or killing of a brood member, could be documented (Mock 1994). To determine if disruption of growth was associated with the incidence of siblicide in a brood, I compared mass changes of individual nestlings from siblicidal broods to that for nestlings from nonsiblicidal broods for which at least two members survived to day 24. I eliminated autocorrelation between consecutive observations by calculating ordinary first differences between observations (Neter et al. 1985). I then calculated average mass change and the respective standard deviation from these differenced observations; standard deviations were $\log_e$-transformed before analysis. These calculations were performed separately for age classes II and III. I tested whether mass gain and variation in mass gain differed between siblicidal and nonsiblicidal broods and between age class by two-factor ANOVA.

Significance tests were specified for an α of 0.05; the power of the test (the probability of correctly rejecting a false null hypothesis of no difference between groups) was given by 1 − β (Steel and Torrie 1981). All statistical procedures were performed in SPSS for Windows (Norusis 1993).

RESULTS

Causes of death.—In six instances, the entire brood (brood size, $\bar{x}$ = 4.5 ± 0.5) disappeared simultaneously; in these cases, young were less than 15 days old. Loss of two complete broods was due to predation by Common Ravens (*Corvus corax*). Partial brood loss occurred in 18 of the remaining 19 broods; 62 of 117 nestlings died or disappeared from time of hatching to time of fledging.

When cause of death could be determined, nonpredation nestling mortality usually could be attributed to either starvation (i.e. a consistent failure to gain mass and progressive emaciation) or siblicide (i.e. where at least one nestling in a brood was injured or killed by nest mates; Mock 1994). Two nestlings apparently choked to death on food items too large to swallow.

Starvation accounted for at least 30 deaths. "Starvelings" tended to hatch between one to three days later than survivors. Most starvelings (n = 25) died before day 16 posthatching; four young hatched more than two days after other brood members died within three days of hatching. Extensive bruising on the head and nape was noted for 12 dead or moribund starvelings in nine broods; these injuries were noted only for very young nestlings (i.e. during the first nine days posthatching).

Siblicide was implicated in the deaths of at least five nestlings in two broods, and possibly in the deaths of nestlings in three other nests (Appendix). Severe laceration injuries were noted for nine nestlings in these five broods; these injuries were observed on the lateral and synsacral areas and upper thigh, and occasionally resulted in penetration of the visceral cavity, and disembowelling. Siblicidal episodes occurred in broods where nestlings were between 15 and 24 days of age.

Survival and brood size.—Mean clutch size was 6.4 ± SD of 1.0 for 25 broods; brood size averaged 4.7 ± 1.5 young at the time of hatching (Fig. 1).

The Kaplan-Meier cumulative survival functions indicated that brood size at hatching influenced nestling survival of magpies in this population (Fig. 2A). The survival distribution for broods of three was significantly lower than that for broods of five (U = 17.06, P < 0.001) and six (U = 8.43, P = 0.037); all remaining comparisons were not statistically significant (P > 0.2). The probability of a nestling surviving to fledging age was approximately 0.63 for nestlings from broods of five, 0.42 for broods of four, six, and seven, and 0.00 for broods of three (Fig. 2A). Median survival time was longest (21 days) for broods of five, and shortest (8.7 days) for broods of three; intermediate median survival times (15 to 17 days) were exhibited by broods of four, six, and seven young at hatching (Fig. 2B).

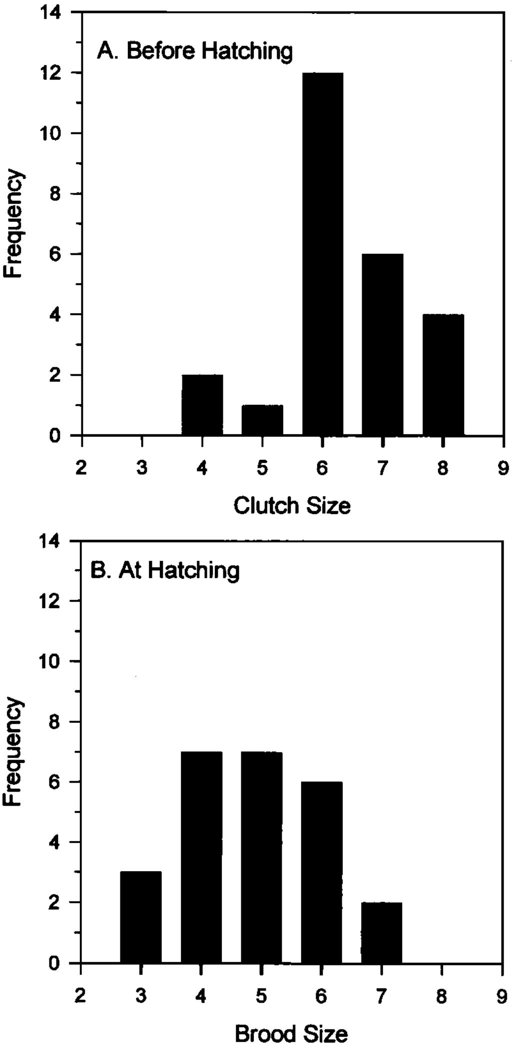

Fig. 1. Frequencies of (A) clutch size and (B) brood size at hatching for Black-billed Magpies.

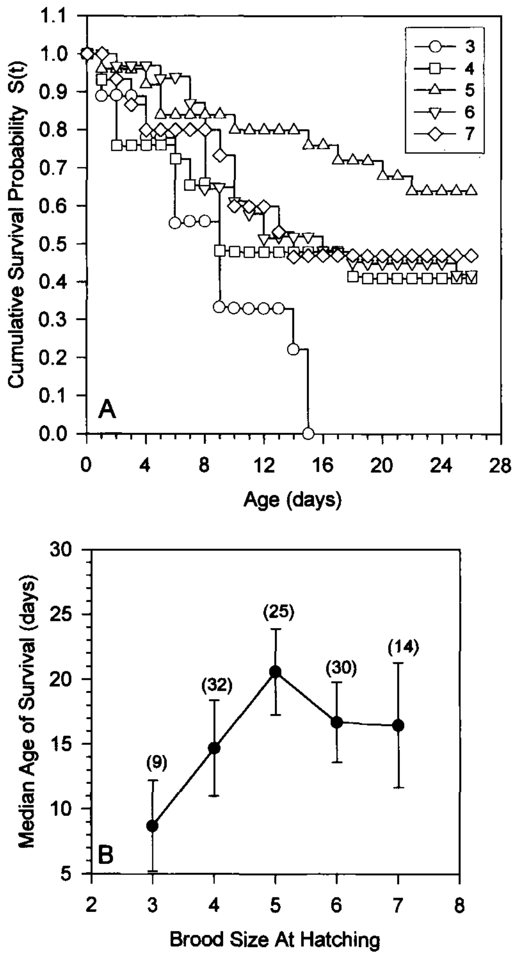

Fig. 2. Effects of brood size at hatching on survival of Black-billed Magpie nestlings. (A) Kaplan-Meier estimates of cumulative survival probability; (B) median survival time of individual nestlings. Error bars represent 95% confidence intervals; number of nestlings shown in parentheses.

An average of 2.1 ± 2.0 young in 15 broods survived to day 24. No young fledged from broods of size three at hatching ($n = 3$ broods). There was no statistically significant effect of brood size on the proportion of young fledged from larger broods ($X^2 = 2.45$, df = 3, $P > 0.2$).

Survival and weather.—The probability of nestling death was affected strongly by environmental variables, independent of brood size ($P > 0.2$). The relative influence of weather on nestling survival declined with increasing nestling age. Cox regression models describing the association of various environmental variables with the probability of nestling mortality are given in Table 1 (if criteria for model inclusion were not met, variables were omitted from table). The incidence of rainfall (PRECIP) was the predominant influence on early nestling mortality; the estimated risk of death was twice as great for nestlings if rain occurred on day of hatching and at day 5, before the presumed age of thermoregulatory competence. An increase in the minimum daily temperature (TMIN) reduced estimated risk by 22% for 5-day-old nestlings and by 49% for 20-day-old nestlings. Wind significantly affected survival of day-10 nestlings; estimated risk increased by 1.3 times on windy days.

Survival and morphometrics.—Increased intraclutch variation in egg mass (ln CV) was positively, but weakly, associated with estimated brood survival time ($r = 0.19$, $B = -2.006 \pm$ SE of 0.979, $P = 0.040$; Fig. 3).

Hatching intervals between the average for the clutch and the last-hatched young varied between one to three days. Starvelings were always the last-hatched and/or penultimate nestlings in a brood, always grew more slowly than older nest mates, and were smaller and lighter in mass than surviving nest mates at the time of death (Fig. 4A).

Young dying before day 9 (age class I) were significantly smaller in linear dimensions than survivors ($P < 0.025$, and $[1 - \beta] > 0.63$ in all cases); however, the multivariate test on all four linear variables did not result in statistically significant differences between groups (Hotelling's $T^2 = 0.230$, df = 4 and 29, $P = 0.184$, $[1 - \beta] = 0.59$). The mass of dead young was significantly less than that of survivors ($P = 0.010$, $[1 - \beta] = 0.76$; Table 2).

For nestlings of age class II, there were no statistically significant differences in linear dimensions ($T^2 = 1.304$, df = 4 and 5, $P = 0.300$, $[1 - \beta] = 0.39$; univariate tests, $P > 0.40$ and $[1 - \beta] > 0.40$) or body mass ($P = 0.373$) between survivors and dead young.

For nestlings of age class III, the mass of dead young was significantly less than that of survivors ($P = 0.032$, $[1 - \beta] = 0.72$). However dead nestlings did not differ statistically from survivors in linear dimensions ($T^2 = 0.207$, df = 4 and 13, $P = 0.622$, $[1 - \beta] = 0.37$; univariate tests, $P > 0.1$ and $[1 - \beta] > 0.55$; Table 2).

Nestlings in siblicidal broods were characterized by a period of fluctuating mass gain and loss prior to the death of a sibling (Fig. 4B and Table 3). Variation in mass was significantly

TABLE 1. Parameter estimates and association of environmental variables with the probability of survival of nestling Black-billed Magpies, as determined by Cox regression.

Variables	B^a	SE (B)	e^B	$r_p{}^b$	P
Day of hatching (n^c = 110; −2 log likelihood = 501.079, P < 0.001)					
TMIN	−0.110	0.047	0.896	−0.080	0.020
PRECIP	0.777	0.180	2.175	0.177	<0.001
WIND	−0.205	0.112	0.815	−0.050	0.068
Day 5 (n = 107; −2 log likelihood = 485.437, P < 0.001)					
TMAX	−0.173	0.037	0.841	−0.199	<0.001
TMIN	−0.247	0.064	0.781	−0.157	<0.001
PRECIP	0.752	0.194	2.120	0.159	<0.001
Day 10 (n = 87; −2 log likelihood = 344.330, P = 0.062)					
WIND	0.246	0.133	1.279	0.064	0.064
Day 20 (n = 52; −2 log likelihood = 24.707, P = 0.041)					
TMIN	−0.670	0.337	0.512	−0.248	0.047

[a] Cox regression coefficient.

[b] Partial correlation of independent variable with expected death rate at time t.

[c] Number of nestlings at each age.

greater in siblicidal broods as compared to nonsiblicidal broods (F = 8.47, P = 0.005), and was significantly greater in younger (age class II) nestlings (F = 38.12, P < 0.001). In contrast, average mass gain did not differ between siblicidal and nonsiblicidal broods for either age class (F = 1.00, P = 0.321). As expected, mass gained by younger (age class II) nestlings that are still growing was significantly greater (F = 101.24, P < 0.001) than that of older nestlings, which were approaching the growth asymptote.

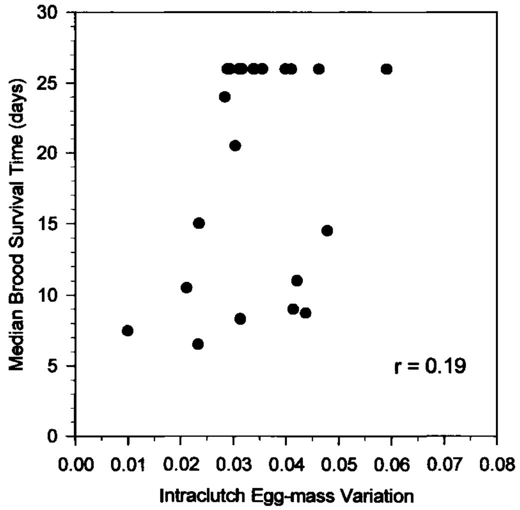

Fig. 3. Association of median brood survival time and intraclutch egg-size variation for 22 Black-billed Magpie broods.

Average mass of nestlings surviving to 24 days of age was negatively correlated with brood size at fledge (r = −0.70, P < 0.01, n = 15 broods). There was a negative association between linear measurements and brood size at fledging; however, correlations were too weak for statistical significance (head length, r = −0.25; culmen length, r = −0.21; manus length, r = −0.44; tarsus length, r = −0.29).

DISCUSSION

For Black-billed Magpies in my study, there was variation within a single nest, as well as within the population as a whole, in both the incidence and the timing of specific types of brood-reduction. Both starvation (passive sibling competition) and siblicide (active and aggressive sibling competition) were implicated in nestling mortality, as were certain modes of parental control, such as egg-size variation, hatching asynchrony, and possibly infanticide. However, the significant impact of abiotic factors on nestling mortality, independent of brood size, suggested that brood reduction was not necessarily under the direct control of either offspring or parents. Although brood reduction refers specifically to adaptive mechanisms controlling brood size (Mock 1994), probabilities of nestling survival may be equally influenced by nonadaptive factors, such as weather.

Parental control of brood reduction is manifested by active infanticide (Trail et al. 1981, Stanback and Koenig 1992), as well as by vari-

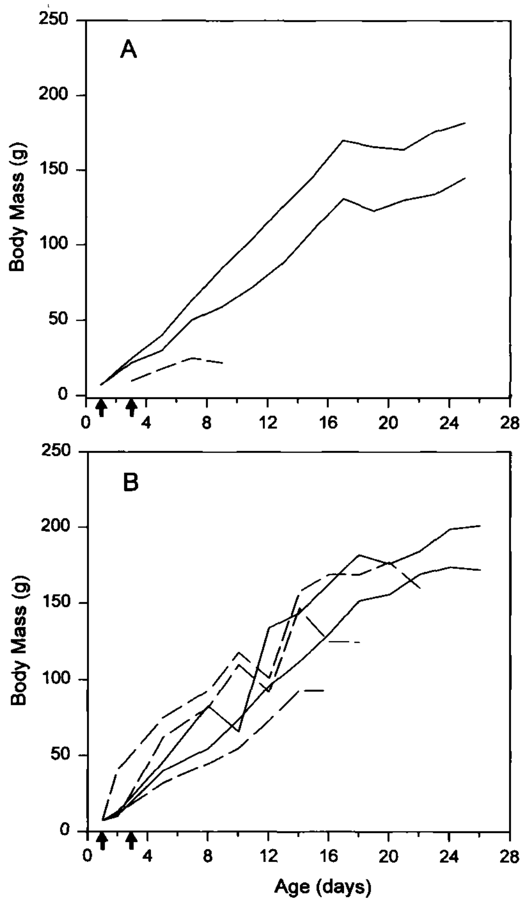

Fig. 4. Patterns of body mass gain in magpie broods typifying brood reduction through either starvation or siblicide. Solid lines indicate young surviving to day 24; dotted lines indicate young dying before day 24; arrows indicate time of hatching. (A) Brood reduction through starvation of the youngest nestling. The dead nestling hatched two days after its surviving nest mates. (B) Brood reduction through siblicide; note fluctuating mass gain and loss in week prior to nestling death.

Table 2. Mean morphological measurements (± SD) for surviving and dead Black-billed Magpie nestlings in age classes: (I) ages 0 to 8 days; (II) ages 9 to 15 days; and (III) ages 16 to 24 days.

Variable	Survived	Died	P^a
	Age class I (n^b = 34)		
Head (mm)	33.21 ± 6.46	29.61 ± 8.89	0.019
Culmen (mm)	13.02 ± 2.88	10.65 ± 3.08	0.024
Manus (mm)	19.70 ± 6.47	14.95 ± 6.26	0.021
Tarsus (mm)	21.90 ± 7.17	15.99 ± 6.72	0.014
Mass (g)	51.1 ± 25.3	30.3 ± 26.4	0.010
	Age class II (n = 10)		
Head (mm)	43.78 ± 5.96	41.29 ± 8.59	0.550
Culmen (mm)	17.52 ± 2.43	17.03 ± 4.00	0.731
Manus (mm)	33.13 ± 7.39	28.86 ± 11.50	0.406
Tarsus (mm)	34.41 ± 5.98	30.60 ± 9.41	0.402
Mass (g)	95.8 ± 32.8	78.4 ± 44.4	0.373
	Age class III (n = 10)		
Head (mm)	58.51 ± 3.83	56.35 ± 4.26	0.266
Culmen (mm)	24.00 ± 2.32	22.99 ± 2.34	0.372
Manus (mm)	48.16 ± 1.83	45.52 ± 3.89	0.089
Tarsus (mm)	47.72 ± 1.52	46.53 ± 2.44	0.230
Mass (g)	169.4 ± 14.2	145.9 ± 24.1	0.032

[a] Probability obtained from one-tailed t-tests on $\log_e$-transformed variables.

[b] Number of comparisons for dead young and average for surviving siblings in a brood.

ation in egg size within a clutch (Slagsvold et al. 1984) and hatching asynchrony (Lack 1954, 1968, Ricklefs 1965, Mock 1994). Parental manipulation of brood size may increase parental fitness by affecting both the number of young surviving to fledging and the number of young surviving to independence (Husby 1986).

It was not possible to determine if adult magpies deliberately killed young. However, direct parental involvement in early nestling mortality was suggested by injuries observed for 12 nestlings under nine days of age. Active killing of young has been observed in other corvid species; for example, adult female Piñon Jays (*Gymnorhinus cyanocephala*) have been observed to kill and eat their own hatchlings (Balda and Bateman 1976). However, the bruising observed on the heads of young magpie nestlings is equally consistent with observations that the female encourages nestling begging response by tapping nestlings on the head (Goodwin 1986), and by attempts to force feed young (Bengtsson and Ryden 1981). It is possible that

Table 3. Mass gain (g) and variability (g; SD) in mass gain in Black-billed Magpie nestlings from siblicidal and nonsiblicidal broods.

Variable	Brood status[a] Non-siblicidal	Siblicidal
	Age class II	
Average mass change	9.5	9.6
Variation in mass change	10.3	17.0
	Age class III	
Average mass change	3.8	1.8
Variation in mass change	7.1	6.8

[a] For nonsiblicidal broods, n = 31 (nine broods). For siblicidal broods, n = 12 (five broods).

more intense efforts to stimulate a weak or moribund nestling could kill it.

Differences in nestling size may be initiated by differences in egg size within a clutch; a relationship between egg size, initial nestling size differences and concomitant nestling survival have been demonstrated for Snow Geese (*Chen caerulescens;* Ankney 1980), as well as certain passerine species (O'Connor 1975, 1979). The relationship between intraclutch egg size variation and nestling survival is suggested by comparative eagle data; those species characterized by obligate siblicide showed a greater degree of intraclutch variation than species exhibiting facultative siblicide (Edwards and Collopy 1983). In magpies, intraclutch egg-mass variation was positively, although weakly, correlated with median brood survival time. This observation is consistent with Slagvold et al.'s (1984) concept of a brood reduction "strategy," which hypothesizes that increased variation in egg size within clutches may be selected for in species with a high incidence of nestling mortality from starvation.

Initial size differences between nestlings are further exaggerated by the spread in hatching times induced by asynchronous hatching. In all species observed to date, early mortality from starvation is influenced by the size hierarchy determined by hatching order within a brood; this effect is exacerbated when parental food delivery rates are inadequate (Bryant 1978). Starvation has been demonstrated experimentally to be the major factor contributing to early nestling mortality of magpies (Högstedt 1981, Hochachka and Boag 1987). In my study, starvation of the youngest and weakest young occurred primarily during the first nine days posthatching, as has been observed in previous studies (Högstedt 1981, Tatner 1984, Hochachka and Boag 1987, Birkhead 1991). When active siblicide has been implicated in nestling deaths, the victim is invariably the smallest and weakest nestling in the brood (Ingram 1959, Fujioka 1985). However, the timing of siblicidal events may be related to the biology of the species in question. In semialtricial species, siblicide generally occurs shortly after hatching of the smallest young (Ingram 1959, Meyburg 1974, Bortolotti et al. 1991); in these species, motor control is established shortly after hatching. In contrast, siblicide in magpies appears to occur only during the last trimester of the nestling period, when motor coordination was well established. At this time, linear size differences between magpie siblings were relatively small, although large mass discrepancies still existed between surviving and dead young. However, the interaction between brood size, nestling age, and environmental factors on the outcome of sibling competition and probability of nestling survival suggests that there is no explicit cause-and-effect relationship.

Morphological data suggested that young that are smaller than their siblings are less likely to survive to fledging. The differences in linear measurements between surviving and dead young were not statistically significant for age classes II and III; however, failure to detect differences in at least some of these comparisons may be partially attributed to the low statistical power ($1 - \beta$) of the tests. Statistical power is determined by the magnitude of the difference between groups, sample size, and sample variability. The magnitude of the differences in manus length, tarsus length (ca. 4 mm), and body mass (17 g) for surviving and dead age class II young (Table 2) may be biologically important; however, small sample sizes and large variability precluded statistical detection. In contrast, the smaller (1 to 2 mm) differences observed linear measurements of age class III nestlings are less likely to influence the probability of nestling mortality. Controlled growth experiments are required to determine the practical significance (DeVore 1987) of morphometric differences in relation to nestling risk of mortality.

Overall size differences among nestlings are not the only factor influencing the occurrence of sibling competition. Experimental food supplementation has been demonstrated to increase average number of young magpies fledged per brood (Hochachka and Boag 1987, Dhindsa and Boag 1990). In this study, both nestling mass loss and death were associated primarily with cold and wet weather. Although I did not collect data on food availability or parental delivery rates, it is reasonable to assume that insect availability was greatly reduced and constraints on parental food delivery rates, therefore, could contribute to nestling mortality. Fluctuations in prey densities have been shown to significantly influence nestling survival of American Kestrels (*Falco sparverius*) and other small raptors independently of brood size, supporting the hypothesis that parental ability to feed young is the predominant factor limiting brood size at fledging (Gard and Bird 1992).

Food supply also may influence the incidence of nestling mortality due to sibling aggression. Although there are few experimental data to strongly support the role of nestling hunger as a proximate factor inducing siblicide (Mock 1985), relative food supply has been observed to affect rates of siblicide in small raptors (Bortolotti et al. 1991) and Black-legged Kittiwakes (*Rissa trydactyla;* Braun and Hunt 1983). The rate of siblicide in kittiwakes significantly increased after extended periods of inclement weather (Braun and Hunt 1983). For species exhibiting obligate siblicide, food shortage is not a necessary condition inducing siblicide, nor does food supplementation appear to influence levels of nestling aggression. Instead, it appears that lethal levels of aggression are selected for if food is delivered to young in monopolizable, small units (Mock 1985). Magpies would appear to meet both the prey-size criteria (small, monopolizable food items delivered directly in a bolus) and morphological criteria (tearing bill, pecking response, and motor coordination) necessary for siblicide to occur. However, it is likely that siblicidal attacks in magpies are precipitated by inadequate food delivery rates; the wide variation in mass gain exhibited by magpie nestlings in siblicidal broods supports this contention.

Siblicide (which runs the gamut from active fighting between nestlings to cannibalism) occurs relatively less frequently than other mechanisms of brood reduction. To date, siblicide and sibling cannibalism have been reported primarily for hawks, owls, and ardeids and not for any passerine species (Stanback and Koenig 1992). Both sibling aggression and cannibalism might be expected in any species that dismembers food items, regardless of the average size of prey delivered to young (Bortolotti et al. 1991); siblicide in passerines might be expected during the period in the nestling stage when food demands are greatest and motor coordination is established. For magpies, siblicide and sibling cannibalism have not been reported previously, although cannibalistic behavior of adults directed at another adult conspecific has been observed (Crease 1992). Magpies are primarily insectivorous, but will opportunistically take other animal foods. In common with other corvid species, magpies dismember prey items too large to swallow (Goodwin 1986). The terminal hook on the corvid bill is appropriate for grasping and pinching off pieces of tissue, although it is not specifically adapted as a penetrating weapon (Rowley 1970). Magpies apparently killed siblings by pecking and tearing at the relatively thin, unfeathered skin on the flanks and dorsum; this behavior occurred only during the last week of the nestling period. If siblicide only occurs in magpies during the late nestling period under conditions of limited food, the chances of observing this behavior on a regular basis are low.

Fledging success was influenced by brood size; broods numbering five young at hatching had a substantially higher probability of fledging at least one young than did smaller or larger broods. However, fledgling size (mass and linear measurements) was negatively correlated with brood size. Similar results have been demonstrated experimentally for both American Kestrels (Gard and Bird 1992) and Collared Flycatchers (*Fidecula albicollis;* Gustafsson and Sutherland 1988); more young fledged from enlarged broods, but fledgling size was smaller. In Collared Flycatchers, the main cost of enlarged clutches appeared to be increased juvenile mortality and, therefore, reduced second-generation recruitment (Gustafsson and Sutherland 1988). There is some evidence to suggest that larger and heavier magpie nestlings have a higher probability of surviving at least the first few months after fledging (Birkhead 1991). Thus, there is a complex interaction of factors governing the probability of survival to fledging and factors influencing the probability of survival after fledging. The situation is further complicated by year-to-year variations in environmental conditions and, by inference, food supply and delivery rates. In American Kestrels, low prey densities were associated with higher nestling mortality regardless of nestling body size and brood size; significant between-year effects confounded the effects of experimental brood-size manipulations (Gard and Bird 1992).

Variation in probabilities of nestling survival are influenced by the effects of ambient temperature and precipitation. In other species, environmental effects are associated with impacts on nestling size and survival, and may be induced either by direct effects of exposure on unprotected nestlings, or indirectly by effects on food supply (Murphy 1985). The interaction of ambient conditions with (presumably) adaptive phenotypic traits characteristic of brood reduction suggests the potential confounding of evolutionary and nonevolutionary processes. These considerations will have important implications for future determinations of brood reduction strategies in wild populations.

ACKNOWLEDGMENTS

I thank F. Bucknam, C. Wright, T. and J. K. Lloyd, and J. and C. Shepard for permission to work on their land. I am grateful to R. Bowlds, R. M. Lee III, P. Ziegler, and especially J. K. Lloyd and J. R. Lloyd for field assistance. I thank P. Kukuk for key references, and R. M. Lee III and several anonymous reviewers for valuable comments and suggestions that greatly improved the manuscript.

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APPENDIX

Siblicide and Sibling Cannibalism in Black-billed Magpies.

Siblicidal events were observed between 19 May and 4 June 1994. During this time, rainfall totalled 0.55 cm, and occurred on 11 of 17 days; rainfall levels were normal for this time of year. The average daily air temperature was 13°C, and the mean daily maximum and minimum temperatures were 21° and 6°C respectively; temperatures were below normal for 10 of 17 days.

In one nest, the smallest nestling (aged 20 days) had been killed and disembowelled by one or both of its larger siblings; it was still warm when found, and the gut was being pulled out of the body cavity by the largest nestling. The largest nestling regurgitated small pieces of flesh when handled. The dead nestling weighed 124 g as compared to an average of 177 g for the survivors. Two days later, the smaller of the two surviving nestlings was apparently driven out of the nest by its larger sibling, and was found on the ground, alive but seriously injured with the right femur stripped completely of skin and muscle and several small lacerations over the right synsacral region. This nestling had lost 25 g over the previous four days, and had a mass 35 g less than the aggressor at the time of the attack. Previously, two other nestlings had died at days 9 and 11, respectively, after a prolonged period of mass loss. The single survivor fledged successfully at 26 days, and was observed within 30 m of the nest tree on day 40.

In the second nest, a 16-day-old nestling was found dead and partially dismembered at the bottom of the nest cup. Although it had hatched within 12 h of its siblings, it weighed only 93 g at the time of its death, as compared to the average mass of 150 g for the four survivors. Two days later, a second dead nestling was found in the nest, disembowelled with the gut partly eaten. Two survivors had extensive bruising and open ragged wounds over the left synsacrum; the third nestling had wounds on the right tibiotarsus. The extent of wounding on nestlings increased over the next six days. On day 24 the middle nestling was found dead and partly eaten; the smallest nestling was seriously injured, the entire right femur being completely stripped of flesh, and the extremities cold and without motor control. The injuries on the largest nestling had scabbed over. Both nestlings survived to leave the nest at 28 days. However, the smaller survivor was incapable of perching and, although I observed it on two occasions being fed on the ground by at least one parent, it disappeared approximately one week after leaving the nest.

In three other broods, dead nestlings had disappeared before they could be examined. However, all nestlings had been wounded prior to disappearance. In two cases, the nestling's color band and the gizzard were found in the nest lining. One nestling fledged from each of these three nests.