Offspring reproductive value and nest defense in the magpie (*Pica pica*)

Tomas Redondo and Juan Carranza

Cátedra de Biología y Etología, Facultad de Veterinaria, Unex, 10071 Cáceres, Spain

Received January 22, 1989 / Accepted June 5, 1989

Summary. Magpie (Pica pica) brood defense against a human at the nest was studied in a Mediterranean population with low renesting potential. Variations in two defense measures recorded during 106 trials at 41 different nests were positively correlated with brood age. Incremental effects due to the number of successive visits to nests by us, brood size, and the time in the breeding season were not significant. Partial correlation analyses showed that visit rate was not an important determinant of nest defense, which thus favors an adaptive explanation of nest defense patterns. Two functional hypotheses to account for the increase in defense intensity with brood age were tested: whether (1) increased parental defense serves to compensate the higher predation risk of older nests or (2) increased parental defense reflects the increasing reproductive value of nestlings as they grow older. Daily mortality and incidende of predation (estimated from contribution of wholebrood losses to total mortality) was higher early in the nestling period, hence providing weak evidence for the assumption on which hypothesis (1) is based. The timing of parental defense intensity did not mirror variations in predation risk for the nest but variations in reproductive value of the brood, as can be estimated from daily mortality. thus supporting hypothesis (2). Magpie parents increased defense intensity in response to premature escaping by almost fully-developed nestlings. Since such a response lowers predation risk for the offspring and increases their probability of survival. this finding supports hypothesis (2), but runs contrary to hypothesis (1). Parents also increased defense in response to play-backs of alarm calls uttered by nestlings during escaping episodes. It is argued that parents should continuously monitor

the degree of offspring development in order to assess their reproductive value and that, by alarm calling, chicks honestly make their parents aware of the gain in reproductive value that results from enhancement in locomotory abilities that occur at the end of the nestling period.

Introduction

Parental behavior involves, for many animals, some form of offspring protection against predators. Predation is the main source of mortality among nestlings of altricial birds (Ricklefs 1969), thus selection should have acted on parents to reduce predation pressures. Repeatedly, investigators have reported an increase in both frequency and strength of parental anti-predator behavior as a function of age of the brood (see Montgomerie and Weatherhead 1988 for a historical review). Functional explanations for this phenomenon have attributed the increasing trend in nest defense with offspring age either to the higher predation risk incurred by older nestlings (Skutch 1976; Greig-Smith 1980) or to the increasing value to parents of the current brood relative to future ones (Trivers 1972; Barash 1975; Andersson et al. 1980; Curio et al. 1984), as is predicted by the parental investment decision theory (Coleman et al. 1985). Further refinements on this last theory (Dawkins and Carlisle 1976; Boucher 1977) have stressed the view that parents should not rely on the amount of past investment (but see Coleman et al. 1985), but on prospective reproductive value of their offspring when making decisions about allocation of parental effort (cf. Trivers 1972). As a current brood becomes older, its relative reproductive value increases. Such an increment was formerly thought to mirror the decreasing prospects for par-

Offprint requests to: T. Redondo

370

ents to reinitiate a subsequent breeding attempt within the same breeding season (Barash 1975). However, as long as single-brooded species that also fit this pattern are found (Reid and Montgomerie 1985), the influence of offspring age upon the relative value of a brood probably reflects a decreasing difference between survival expectancies of parents and their offspring as the young get closer to the next breeding season (Andersson et al. 1980).

These two hypotheses lead to several testable predictions. According to the "Predation Risk hypothesis," older nests suffer from increased predation as a consequence of two factors: older nests are more conspicuous (because chicks beg louder and are fed at a higher rate) and more profitable to predators due to nestling growth (Greig-Smith 1980). Consequently, it assumes higher nest losses caused by predators late in the nestling period. The "Reproductive Value hypothesis" predicts that defense levels increase in response to any developmental change that causes an increase in nestlings' probability of survival (Patterson et al. 1980). During development, nestlings cross through certain "bottleneck" phases, after which some causes of mortality become reduced (i.e., thermal stress after attaining homeothermy or starvation after reducing growth or metabolic rate; O'Connor 1984). The young of many bird species can scramble out of the nest before they actually fledge in order to evade predators (Clark and Wilson 1981). All these factors suddenly increase the offspring's probability of survival until the next breeding season, hence their reproductive value. The ability of nestlings to abandon the nest prematurely appears to be specially useful for testing our two hypotheses because, as a consequence of self-protective behavior, predation risk becomes highly reduced. The Predation Risk hypothesis predicts a decrease in parental defense in response to the escaping behavior of nestlings while the Reproductive Value hypothesis predicts an increase in investment under the same conditions. In a study about nest defense in stonechats Saxicola torguata, Greig-Smith (1980) suggested that reproductive value explained nest defense better than predation risk but this conclusion was supported by indirect evidence and none of the two hypotheses could be rejected.

These two hypotheses do by no means exclude each other, since both predation risk and reproductive value of the brood can increase with nestling age. However, it is of interest to ascertain what the most powerful predictor of nest-defense patterns is, since data on nest defense have been often used for testing more general predictions of lifehistory and parental investment decision theories (Robertson and Biermann 1979; Weatherhead 1979; Carlisle 1985; Coleman et al. 1985; Lazarus and Inglis 1986).

An alternative explanation for the increasing pattern of nest defense with offspring age has been offered by Knight and Temple (1986a). Most studies of nest defense involve revisitation of the same nest. Parents may become positively reinforced by their "success" in driving away intruders with no damage to themselves and their broods and therefore defend more willingly the next time the intruder appears (Knight and Temple 1986a, c). Such a causal explanation should, in theory, not conflict with functional ones, unless evidence for an increase in defense intensity with offspring age could be proven to be all but a methodological artifact. Some studies on naive nests have reported an increasing pattern of nest defense (Shalter 1979; Patterson et al. 1980; Röell and Bossema 1982; Regelmann and Curio 1983; Stephens 1984; Curio 1987; Kilpi 1987). In fact, positive reinforcement of parents can be predicted by a life-history model of optimal investment in nest defense by assuming that parents can assess the risk posed by a predator as a function of past experience (Redondo, in preparation). This could explain why a greater amount of variance in defense levels is explained by accounting for both offspring age and visit rates simultaneously than by any of the two separately (Breitwisch 1988).

Magpie (Pica pica) parents invest time and energy in defending their nests against predators (Linsdale 1937; Erpino 1968; Verbeek 1973; Röell and Bossema 1982; Buitron 1983). In doing so, they enhance brood survival at a cost to themselves of being injured or killed by predators (Buitron 1983). They also increase nest defense as offspring get older (Erpino 1968; Röell and Bossema 1982; but see Buitron 1983); shortly before fledging, nestlings show premature escaping behavior in response to disturbances (Linsdale 1937; Röell and Bossema 1982). In the Spanish population studied by us, median laying and fledgling dates occurred on April 20th and June 12th, respectively. These dates are similar to those obtained from other populations (Erpino 1968; Högstedt 1981; Tatner 1982; Eden 1985a). However, unlike for northern populations, prospects for reinitiating replacement clutches are negligible for most Mediterranean magpies since summer drought removes most green vegetation and caterpillar biomass from early July on. We were then led to ask three questions about magpie nest defense in a virtually single-brooded population:

(1) What is the timing of nestling mortality? Indirectly, the analysis of age-dependent mortality would inform us about the incidence of predation as a function of offspring age.

(2) Do parental levels of defense mirror offspring's probability of survival or risk of being preyed upon?

(3) Does defense level increase (decrease) in response to premature escaping by nestlings?

Methods

Mortality

During the 1984 and 1985 breeding seasons, we monitored the reproductive histories of 144 pairs for which hatching dates were known within a margin of error of ± 1 day. This error is due to asynchronous hatching within a brood; therefore, brood age was assigned to one of ten 3-day age classes for covering the whole nestling period (up to 29 days). Nests were visited every 2 days whenever possible. From this sample, we obtained data on 52 nests (266 hatchlings) for which loss dates could be accurately assigned to one age class. Daily mortality for each age class was calculated according to Ricklefs (1969), both for within-brood and whole-brood losses. Typically, whole-brood losses are the result of predation (Ricklefs 1969), hence contribution of whole-brood losses to total was used to estimate differential predation risk by age.

Nest defense measurement

Nest defense trials. In the spring of 1986, we recorded nest defense behavior of unmarked breeding magpies from the birds' response to one of us (TR) as a potential nest-predator. Since we had to inspect nests during laying and incubation in order to determine hatching dates, all trials were conducted with revisitated nests. During the nestling period, dates for defense trials were established on a random basis, thus allowing for enough variability in the number of successive visits to a nest. Familiarity with human individuals, including their posture, has been shown to affect nest defense responses (Buitron 1983; Knight and Temple 1986b). We tried to homogenize results at different nests by leaving both the individual and his clothes unchanged. On the other hand, Röell and Bossema (1982) did not detect differences between the proportion of nests defended against a human being and the proportion defended against a caged crow. After arrival at the nest-tree, each trial, which included climbing to the nest, lasted for 10 min. Once at the nest, data were collected by softly speaking into a clip condenser microphone attached to a cassette recorder. Nests were observed continuously, except for momentary interruptions to locate adult birds. We conducted 106 trials at 41 different roofed nests. Seven unroofed nests were discarded, since differences in defense responses between roofed and unroofed nests had been detected elsewhere (Röell and Bossema 1982).

Dependent variables. During each trial, we recorded scolding by defending birds in order to calculate "Calling Rate" (number of rattles per unit time). In magpies, scolding rate has been found to be highly correlated with attacking, so it is a good indicator of the birds' willingness to defend (Röell and Bossema 1982; cf. Buitron 1983). In the field we also measured "Latency to Approach and Scold" by using a stopwatch. Finally, we assessed "Proximity to the human" by scoring minimum distance attained on a subjective basis: 4 (perched at the nest tree), 3 (perched at an adjacent tree or flying between it and the nest), 2 (perched or flying between the nearest and the second-nearest tree), 1 (further than 2), and 0 (no response was detected). Trees in our study area (a cleared oak wood) were regularly spaced at distances ranging from 60 to 110 m.

Independent variables. We looked for significant correlations between defense measurements and: (1) brood age, estimated within 3-day age classes; (2) number of previous defense trials to which the nest had been exposed before; (3) total number of previous visits to the nest; (4) brood size when a trial was conducted, and (5) time in the breeding season calculated on a continuous scale whereby May 1st=1.

Offspring escaping episodes. Premature escaping by nestlings occurred in 15 nests. When escaping, nestlings jumped out of the nest cup while uttering alarm calls. An alarm call consisted of a series of 2–3 brief, harsh elements. Nestlings can also give distress screams if seized by humans, but no such calls were heard during this study. We separately calculated the parental calling rates before and after chicks gave the first alarm call. Since escaping and alarm calling by nestlings elicited strong defensive responses by adults, we considered only parental calling rates before nestlings escape when calculating correlation coefficients between Calling Rate and independent variables; this was done in order to isolate the effect of the escaping behavior of nestlings.

We were interested in whether parents caring for young nestlings would respond to alarm calls of escaping chicks. Playback experiments were conducted on a sample of 23 nests. These nests were found on the hatching day; therefore, they had received only a single visit before the trial was conducted. The taped stimulus was a sequence of three nestling alarm calls recorded from an escaping episode in 1985 with a UHER 4200 Report Monitor tape recorder. The same recorder and a horn speaker placed on the ground just below the nest was used in play-back trials. The stimulus was presented twice, at 3 and 6 min after reaching the nest tree. Trials lasted for 10 min following arrival at the nest tree.

Data analysis

In those trials for which no visible response occurred, both Calling Rate and Proximity were scored 0, but they were lacking for analyses involving Latency to Approach and Scold in addition to 16 trials for which latency measurements could not be accurately determined. Since no variable fulfilled the normality criterion, non-parametric statistical tests were used following Conover (1980). Partial correlation coefficients calculated over ranks between any single dependent variable and independent variables were employed to determine the relative contribution of independent variables to explain variations in each dependent one. Typically, this method yields results that parallel those of parametric multiple correlation, although it is less powerful (Conover 1980).

Results

Mortality

Magpie nestlings suffered from a higher mortality earlier in the nestling period than in the last days of nest life (Fig. 1).



Fig. 1. Daily mortality of magpie nestlings as a function of brood age calculated over within-brood losses (dotted line) and total losses (continuous line), which include both within- and whole-brood losses



Fig. 2. Probability of a magpie nestling being alive at fledging time as a function of brood age. Dotted line: considering only within-brood mortality. Continuous line: considering both within- and whole-brood mortality

Partial losses were highest during the first few days after hatching and negligible during the last week of nest life. Whole-brood losses also were highly reduced during the second half of the nestling period. Incidence of predation is maximal at age-class 8 days (36% of all whole-brood losses). Consequently, the probability of a nestling of a given age being alive at fledging is much higher for nestings older than 12 days than for younger ones and reaches virtually 1.0 after the age of 23 days is reached (Fig. 2).

Nest defense patterns

Parental defense increased with age of the brood in a non-linear way, showing a sharp increase in both frequency and two intensity measurements



Nestling age (Days)

Fig. 3. Temporal pattern of magpie nest defense during the nestling period as measured by two intensity measures (Calling Rate and Proximity) and by the proportion of nests of a given age showing some defense level. Bars denote standard errors around means (Calling Rate, Kruskal-Wallis ANOVA H= 21.14, df=7, P<0.01; Proximity, Kruskal-Wallis ANOVA H= 16.33, df=7, P<0.05; Percentage of defending nests, Spearman's r=0.83, N=8, P<0.02). Nonlinear regression equation for mean values of Calling Rate, $y=0.27+0.002 x^{0.05}-0.004 x^{0.03}$, $r^2=0.96$, F=22.7, df=5.3, P<0.02; for Proximity, $y=0.65+0.02 x^{1.77}-0.042 x^{1.36}$, $r^2=0.85$, F=15.9, df=5.3, P<0.05

when nestlings were older than 18 days and peaking at the end of the nestling period (Fig. 3). The third defense measurement, Latency to Approach and Scold, showed no consistent pattern with respect to brood age. It showed a weak correlation with Calling Rate (Spearman's r = -0.37, df = 29, P < 0.05) but not with Proximity (r = -0.24, df = 29, ns), in spite of the fact that these two measurements were highly correlated with each other (r = 0.87, df = 104, P < 0.001). In fact, Latency to Approach and Scold showed no significant linear or partial correlation with any other variable, therefore it has been excluded from Table 1. However, considering only those trials for which some level of parental response occurred, Latency to Approach values differed as expected for extreme values of Proximity (Fig. 4).

Table 1 shows that brood age explains a higher amount of variability in Calling Rate and Proximity ranks than the number of visits to a nest or time in the breeding season. Partial correlation coefficients make this point clearer, showing that time in the breeding season has no effect upon defense intensity and that the total number of visits to a nest has a weaker effect (although not significant) when brood age is kept constant. Simple significant correlations between time in the season and visit rate and defense intensity can be thus considered a secondary effect of independent variables being highly correlated with each other.

Offspring self-defensive behavior

Nestlings younger than 13 days typically responded to us by begging for food. Older ones, however, showed fear responses to human intrusion by crouching into the nest and keeping quiet. Crouching inhibited movements of nestlings, which forcibly grasped their claws into the nest bedding. Such a passive defensive response became suddenly substituted by active escaping and alarm calling when chicks were older than 18 days. Virtually all nestlings older than 24 days jumped out of the nest (Fig. 5). They climbed to the highest branches far away from the nest and uttered alarm calls, trying not to fall to the ground. Falling is probably costly since the locomotory skills of the nestlings are not yet fully developed, and, therefore, the birds may be highly vulnerable to ground predators. Furthermore, in 4 out of 37 escaping episodes recorded during our study, nestlings that fell onto the ground suffered from broken legs. If they managed not to fall from the tree, they returned to the nest after disturbance ceased.

Adult birds displayed strong defensive reactions in response to premature escaping by nestlings. Considering only those trials during which nestlings showed some kind of self-defensive response (N=32), parental defense occurred in 15 out of 18 trials in which nestlings escaped (83%)



Fig. 4. Covariation between defense measures. Trials for which Proximity was scored zero are not included. Vertical bars denote standard errors around means (Calling Rate, Kruskal-Wallis ANOVA H = 26.02, df = 3, P < 0.001, N = 47; Latency, Kruskal-Wallis ANOVA H = 8.03, df = 3, P < 0.05, N = 31)

Table 1. Simple Spearman's rank correlation, r_S , and partial rank correlation, r_P (df = N-6), coefficients between variables. Sample sizes N = 106 except for Latency to Approach and Scold (N = 31)

		Indepen	Independent Variable			
		Brood Age	Brood Size	No. previous trials	No. previous visits	Time in the season
Indepen	den	t variable:				
Brood age	r _s		-0.03	0.67***	0.37***	0,65***
Brood size	r _s			-0.22* -	-0.20* -	-0.20*
No. pre- vious trials	·r _s				0.62***	0.69***
No. pre- vious visits	- <i>r</i> _s					0.78***
Depende	ent	variable:				~~~~~
Calling rate	r _s r _P	0.42*** 0.23*	0.04 0.10	0.34*** 0.02	0.30** 0.12 -	0.36*** -0.01
Prox- imity	r _s r _P	0.34*** 0.26**	0.02 0.04	0.23* -0.05	0.23* 0.16 -	0.25** -0.08
Latency	r _s r _P	$-0.09 \\ -0.07$	-0.24 -0.06	0.06 0.00	0.27 0.15 -	0.08 - 0.02

* P<0.05; ** P<0.01; *** P<0.001



Fig. 5. Percentage of broods of a given age displaying self-protective responses against a human intrusion at the nest (N=51 nests)



Fig. 6. Defense responses of magpies caring for broods aged 7-12 days (N=11) and 13-18 days (N=12) before (B) and after (A) presentation of the playback stimulus. Bars denote standard errors around means (Wilcoxon signed-rank test: Calling Rate, broods 7-12 days old, Z=2.93; broods 13-18 days old, Z=3.06; Proximity, broods 7-12 days old, Z=2.09; broods 13-18 days old, Z=3.06). * P<0.05; *** P<0.001

and in 7 out of 14 trials in which nestlings crouched (Fisher's test, P=0.059). Defending parents increased their calling rate in response to the escaping behavior of nestlings. Mean calling rate increased from 4.14 ± 1.5 (SE) to 9.62 ± 1.75 (SE) calls/min after nestlings escaped and gave their first alarm call (Wilcoxon test, V=4, Z=2.75, P<0.01).

Play-back trials

Alarm calls uttered by nestlings during escaping episodes were a sufficient stimulus for increased nest defense by adults. Parents increased both Calling Rate and Proximity in response to taped alarm calls of nestlings – including those parents caring for broods whose age was well below the time at which premature escaping occurs (Fig. 6).

Discussion

Reliability of defense measurements

It is worth questioning, as a first step, the validity of defense measurements as reliable estimators of parental willingness to defend offspring. Proximity to predators probably reflects parental risk accurately (Curio and Regelmann 1985; Curio et al. 1983; Knight and Temple 1986b). Rates of alarm calling, however, pose particular problems. In some species, calls warn the mate or the offspring (Greig-Smith 1980; East 1981; Knight and Temple 1986c, 1988) and hence may be independent from attacking rates. Buitron (1983) argued that an increase in call rate may reflect an increased need for parents to quiet nestlings as they grow older and louder in order to conceal nest location. This hypothesis does not explain, however, why parents increase their calling rates in response to nestling alarm calling, since fear responses inhibit begging, and escaping nestlings make themselves conspicuous. Even genuine alarm calls are energetically cheap, and their rate can be varied at a constant risk level (Mclean et al. 1986). However, increasing calling rate together with proximity may reflect defense level, as long as it serves to intimidate the predator (Curio and Regelmann 1985) or inform it about parents' willingness to attack (Röell and Bossema 1982). At least for magpies, scolding rate can be validated as an estimate of parental willingness to defend.

The third dependent variable, Latency to Approach and Scold, showed weaker relationships with the remaining ones. Although smaller sample sizes may be the cause (see Methods), it should

be noted that while attacking, approaching, or calling to a predator reflect actual intensity of a defense response, latency variables quantify time prior to responding. Latency times may be affected by factors related to the detectability of a predator attack (distance to the nest, visibility, etc.). Latency measurements can be more reliably employed as estimators of defense level when birds are tested by means of acoustic stimuli, since this procedure enhances detectability, as has been found for great tits (Curio 1987).

Brood defense and predation risk

Magpie nest defense did not increase with nestling age in response to a higher predation risk. Differential mortality by age presumably due to predation was higher early in the nestling period, and parents increased nest defense when nestlings had some chance of escaping a predator attack by themselves. This finding provides evidence running counter to the predation-risk hypothesis. In fact, there is little evidence for supporting the assumptions on which it is based because:

(1) Although loudness of nestling begging calls increases with age (Redondo, unpublished), other factors affecting nest detectability by predators based on nestling begging are involved. Call rates may be lower at the end of the nestling period (Greig-Smith 1980). Also, begging calls are easily located, perhaps as a result of sibling competition for food (Redondo and Arias de Revna 1988), but their locatability is expectedly greater for young, actively growing nestlings, than for older ones. Magpie begging calls have the widest frequency range (hence, probably are best locatable) when nestlings are younger than 7 days, that is, just before the period of highest mortality. Maximum growth rates are attained at about 11 days (Redondo, unpublished).

(2) Parental feeding rates increase with nestling age but not steadily. In many studies, they reach a plateau during the last third of the nestling period (Greig-Smith 1980; Haftorn 1982; Grundel 1987; Moreno 1987a; but see Howe 1979), which probably mirrors a similar pattern of energetic requirements by nestlings (Tiainen 1983a). Also, parents caring for older nestlings may search for food closer to nests, thus enhancing vigilance (Hendricks 1987).

Some other factors may favor increased nest predation at an early age. Nests that are easy to find would be destroyed more rapidly, thus age of a nest may be directly related to the difficulty in locating it; also, growth may restrict the size spectrum of animals that prey upon chicks (Ricklefs 1969). Highest predation rates during the first half of the nestling period have also been found for other species (Holcomb 1972; Willis 1973; Best 1978; Werschkul 1979; Tiainen 1983b). On the other hand, Perrins (1965) found that loudly begging broods were predated upon more often. This would be evidence of an increase in predation risk as a brood gets older and therefore louder.

Perhaps predation was lower later on because parents tending older broods were very effective in nest defense. It is difficult to judge from our data what the actual cause-effect relationship is between defense intensity and predation risk since we have not measured the potential predation pressure but the effective one. However, there is fact that supports our hypothesis: as the young grow up, so does the size of the main predators, and therefore the effectiveness of the defense decreases. Carnivores destroyed four entire broods of welldeveloped chicks in our study area. Olfactoryguided predators, like mammals, probably detect an old brood more readily than a younger one; in addition, most of these predators are nocturnal and dangerous, and parents are probably not very successful in deterring them.

Age-dependent reproductive value of nestlings

Reproductive value of nestlings of a given age is directly measured by the probability of their being alive for their first breeding season, since fecundity is held constant prior to their first reproductive attempt (Pianka and Parker 1975). Mortality of fledglings is usually lower than those of nestlings (Ricklefs 1969; Alerstam and Högstedt 1983). Survival of fledgling magpies is about 1.6 times higher than that of nestlings (Alerstam and Högstedt 1983). Also, overall daily mortality of juvenile magpies from September to April is about 0.004, lower than the mortality occurring during the nestling period [computed from data on first broods given by Eden (1985)]. This means that daily increments in offspring reproductive value are higher before chicks leave the nest than after and that nestlings which manage to fledge gain a considerable amount in future reproductive expectancies (Clark and Wilson 1981). Since mortality risks are negligible several days before fledging (see Figs. 1 and 2; also Holcomb 1969, 1972; Osborne and Osborne 1980; Tiainen 1983b), brood defense should steeply increase shortly before fledging and peak when nestlings leave the nest.

During the course of development, physical capabilities of nestlings increase, with a resulting de-

Age range (days)	DM (days ⁻¹)	Reference
00–04	0.036	Eden 1985a
04–14	0.022	Eden 1985a
00–09	0.035	Tatner 1982
10-18	0.032	Tatner 1982
19–27	0.006	Tatner 1982

Table 2. Daily mortality (DM) of nestling magpies obtained in other studies

crease in daily mortality as chicks become better able to cope with environmental adversities (Ricklefs 1969; O'Connor 1984). Positively-skewed survival curves appear to be typical of altricial nestlings (Young 1963). In 22 out of 29 species reviewed, O'Connor (1978) found that mortality occurred mainly in the early part of the nestling period. Other studies also support this finding (Holcomb 1969, 1972; Willis 1973; Hunt and Hunt 1976; Best 1978; Osborne and Osborne 1980; Tiainen 1983b; Hagan 1986; Gibbons 1987). For the magpie, studies on British populations have also yielded highest mortality early in the nestling period (Table 2). Both starvation and climatic adversities, and perhaps predation risk (see above), can account for increased mortality at early ages. For some species, however, excess mortality due to starvation may occur just prior to fledging (Young 1963; Moreno 1987b).

Since mortality occurs mainly early in the nestling period, those parents not incurring high defense risks until nestlings have overcome the period at which mortality is highest should gain a selective advantage. Therefore, we expect daily rates of increase in nest defense to be high late in the nestling period but low early in the period. That is, the shape of the curve portraying defense level versus brood age should increase exponentially. Most studies providing information in this respect support this prediction (Barash 1975; Curio 1975; Weatherhead 1979; Greig-Smith 1980; East 1981; Breitwisch 1988).

Summarizing, intensity of brood defense in the magpie is much better explained by offspring age than by predation risk for the nest or the degree of parental exposure to a would-be predator. Knight and Temple (1986a) criticized earlier work on nest defense by arguing that previous exposures to experimental predators were not controlled for. By partial correlation analysis, we have shown that visit rate alone is not a good predictor of defense intensity when brood age is kept constant but, conversely, brood age correlates with defense level independently of visit rate. The temporal pattern of defense intensity during the breeding cycle is positively accelerated, as would be predicted assuming that parents respond to changes in offspring reproductive value during the course of development. Finally, parents increased defense level in response to offspring self-protective behavior. All these facts support the view that nest defense is a form of parental investment that maximizes reproductive success of parents; hence, it is sensitive to variations in reproductive value of the offspring.

Parental assessment and offspring advertisement of variations in offspring reproductive value

Having found that reproductive value of nestlings strongly depends upon mortality factors related to development, parents should rely on information other than time from hatching when assessing offspring reproductive value. The reason for this is because development may be retarded as a consequence of an inadequate food supply, among other causes (O'Connor 1984). When Knight and Temple (1986c) interchanged nestlings of different ages between nests, parents actually adjusted their defense level to the new experimental situation. Magpie parents that responded to nestling alarm calls while caring for broods aged 7-12 days seemed to behave the same way. Incidentally, like the outcome of Knight and Temple's (1986c) experiment, this finding provides evidence in favor of parents basing their decisions upon future reproductive expectancies of their brood instead of upon the cumulative investment in them. Additional evidence for this statement comes from the fact that during play-back trials, cumulative investment in offspring remained virtually the same before and after presentation of the stimulus.

Nestlings develop locomotory skills once they enter the final phase of growth. Locomotory abilities manifest themselves rather suddenly (Holcomb 1966) and allow nestlings to perform escaping responses shortly before fledging (Minot 1988). In a similar fashion, replacement of begging by crouching responses develops within a very few days (Schaller and Emlen 1961), perhaps linked to the end of the sensitive period for sexual imprinting when species-specific stimuli are recognized (Bischof and Lassek 1985). Premature escaping by nestlings is a feature common to many species (Bateman and Balda 1973; Leinonen 1973; Woodall 1973; Balph 1975; Lewis 1975; Werschkul 1979). Escaping episodes are commonly accompanied by alarm calling and elicit intense parental defense (Linsdale 1937; Bateman and Balda 1973; Woodall 1973; Curio 1975; McFarland 1984; Marzluff 1985). Sudden improvement of nestling's locomotory skills implies an important increase in offspring reproductive value to which parents should be willing to respond by increasing investment. By uttering alarm calls, nestlings probably inform distant parents about their novel abilities and thus benefit from increased anti-predator defense. Younger nestlings would also benefit from higher parental defense, but parents are selected for investing more in old nestlings than in younger ones. Such a conflict of interests could lead to young chicks to manipulate parental behavior by deceptively mimicking an escaping episode (Trivers 1974), as long as parents can respond to alarm calls of chicks independently of brood age. However, since parents can retaliate by defending the brood if and only if it has actually escaped, honest vocal advertisement by chicks is likely to evolve. Perhaps this explains why nestlings were never observed to give alarm calls while crouching, even when they were manipulated by us.

Acknowledgements. We thank E. Curio, A. Kacelnik and an anonymous referee for highly improving the manuscript, S. Eden for kindly offering us his unpublished data and L. Arias de Reyna and co-workers for many facilities during data collection. R. Marquez revised the English. Financial support came from research funds of Cat. Biologia y Etología, Fac. Veterinaria, UNEX.

References

- Alerstam T, Högstedt G (1983) Regulation of reproductive success towards e^{-1} (=37%) in animals with parental care. Oikos 40:140–145
- Andersson M, Wiklund CG, Rundgren H (1980) Parental defence of offspring: a model and an example. Anim Behav 28:536-542
- Balph MH (1975) Development of young Brewer's blackbirds. Wilson Bull 87:207-230
- Barash DP (1975) Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bull 87:367-373
- Bateman GC, Balda RP (1973) Growth, development, and food habits of young piñon jays. Auk 90:39-61
- Best LB (1978) Field sparrow reproductive success and nesting ecology. Auk 95:9-22
- Bischof HJ, Lassek R (1985) The gaping reaction and the development of fear in young zebra finches (*Taeniopygia guttata castanotis*). Z Tierpsychol 69:55–65
- Boucher DH (1977) On wasting parental investment. Am Nat 111:786–788
- Breitwisch R (1988) Sex differences in defence of eggs and nestlings by northern mockingbirds, *Mimus polyglottos*. Anim Behav 36:62-72
- Buitron D (1983) Variability in the response of black-billed magpies to natural predators. Behaviour 78:209-236
- Carlisle TR (1985) Parental response to brood size in a cichlid fish. Anim Behav 33:234-238
- Clark AB, Wilson DS (1981) Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. Q Rev Biol 56:253-277

- Coleman RM, Gross MR, Sargent RC (1985) Parental investment decision rules: a test in bluegill sunfish. Behav Ecol Sociobiol 18:59-66
- Conover WJ (1980) Practical nonparametric statistics (2 ed). John Wiley and Sons, New York
- Curio E (1975) The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. Anim Behav 23:1-115
- Curio E (1987) Brood defence in the great tit: the influence of age, number and quality of young. Ardea 75:35-42
- Curio E, Regelmann K (1985) The behavioural dynamics of great tits (*Parus major*) approaching a predator. Z Tierpsy-chol 69:3–18
- Curio E, Klump G, Regelmann K (1983) An anti-predator response in the great tit (*Parus major*): is it tuned to predation risk? Oecologia 60:83-88
- Curio E, Regelmann K, Zimmermann U (1984) The defence of first and second broods by great tit (*Parus major*) parents: a test of predictive sociobiology: Z Tierpsychol 66:101–127
- Dawkins R, Carlisle R (1976) Parental investment, mate desertion and a fallacy. Nature 262:131-133
- East M (1981) Alarm calling and parental investment in the robin *Erithacus rubecula*. Ibis 123:223–230
- Eden SF (1985a) The comparative breeding biology of magpies *Pica pica* in an urban and rural babitat (Aves: Corvidae). J Zool London 205:325–334
- Eden SF (1985b) Social organisation and the dispersal of nonbreeding magpies. PhD dissertation, University of Sheffield, Sheffield
- Erpino MJ (1968) Nest-related activities of black-billed magpies. Condor 70:154-165
- Gibbons DW (1987) Hatching asynchrony reduces parental investment in the jackdaw. J Anim Ecol 56:403-414
- Greig-Smith PW (1980) Parental investment in nest defence by stonechats (Saxicola torquata). Anim Behav 28:604–619
- Grundel R (1987) Determinants of nestling feeding rates and parental investment in the mountain chickadee. Condor 89:319-328
- Hagan JM (1986) Temporal patterns in pre-fledgling survival and brood reduction in an osprey colony. Condor 88:200-205
- Haftorn S (1982) Parental care of nestlings by the goldcrest Regulus regulus. Ornis Fenn 59:123-134
- Hendricks P (1987) Foraging patterns of water pipits (Anthus spinoletta) with nestlings. Can J Zool 65:1522-1529
- Högstedt G (1981) Effect of additional food on reproductive success in the magpie (*Pica pica*). J Anim Ecol 50:219–229
- Holcomb LC (1966) The development of grasping and balancing coordination in nestlings of seven species of altricial birds. Wilson Bull 78:57-63
- Holcomb LC (1969) Age-specific mortality of american goldfinch nestlings. Auk 86:760–761
- Holcomb LC (1972) Nest success and age-specific mortality in Traill's flycatchers. Auk 89:837-841
- Howe HF (1979) Evolutionary aspects of parental care in the common grackle, *Quiscalus quiscula* L. Evolution 33:41-51
- Hunt GL, Hunt MW (1976) Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57:62–75
- Kilpi M (1987) Do herring gulls (*Larus argentatus*) invest more in offspring defence as the breeding season advances? Ornis Fenn 64:16-20
- Knight RL, Temple SA (1986a) Why does intensity of avian nest defense increase during the nesting cycle? Auk 103:318-327
- Knight RL, Temple SA (1986b) Methodological problems in the study of avian nest defence. Anim Behav 34:561–566

- Knight RL, Temple SA (1986c) Nest defence in the american goldfinch. Anim Behav 34:887–897
- Knight RL, Temple SA (1988) Nest-defense behavior in the red-winged blackbird. Condor 90:193–200
- Lazarus J, Inglis IR (1986) Shared and unshared parental investment, parent-offspring conflict and brood size. Anim Behav 34:1791-1804
- Leinonen M (1973) On the breeding biology of the white wagtail *Motacilla alba* in central Finland. Ornis Fenn 50:53-82
- Lewis RA (1975) Reproductive biology of the white-crowned sparrow (*Zonotricha leucophrys pugetensis* Grinnell). I. Temporal organization of reproductive and associated cycles. Condor 77:46-59
- Linsdale JM (1973) The natural history of magpies. Pac Coast Avif 25:1-234
- Marzluff JM (1985) Behavior at a pinyon jay nest in response to predation. Condor 87:559-561
- McFarland D (1984) Protection behaviours of breeding whiteplumed honeyeaters *Lichenostomus penicillatus*. Emu 84:42-43
- McLean IG, Smith JNM, Stewart KG (1986) Mobbing behaviour, nest exposure, and breeding success in the american robin. Behaviour 96:171–186
- Minot EO (1988) Sudden reversal of phototaxis during the development of nestling birds. Anim Behav 36:1619–1625
- Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defence by parent birds. Q Rev Biol 63:167–187
- Moreno J (1987a) Parental care in the wheatear Oenanthe oenanthe: effects of nestling age and brood size. Ornis Scand 18:291-301
- Moreno J (1987b) Nestling growth and brood reduction in the wheatear *Oenanthe oenanthe*. Ornis Scand 18:302-309
- O'Connor RJ (1978) Brood reduction in birds: selection for fratricide, infanticide and suicide? Anim Behav 26:79-96
- O'Connor RJ (1984) The growth and development of birds. John Wiley and Sons, Chichester
- Osborne P, Osborne L (1980) The contribution of nest site characteristics to breeding-success among blackbirds *Turdus merula*. Ibis 122:512–517
- Patterson TL, Petrinovich L, James DK (1980) Reproductive value and appropriateness of response to predators by white-crowned sparrows. Behav Ecol Sociobiol 7:227-231
- Perrins CM (1965) Population fluctuations and clutch-size in the great tit, *Parus major* L. J Anim Ecol 34:601-647
- Pianka ER, Parker WS (1975) Age-specific reproductive tactics. Am Nat 109:453–464
- Redondo T, Arias de Reyna L (1988) Locatability of begging calls in nestling altricial birds. Anim Behav 36:653-661

- Regelmann K, Curio E (1983) Determinants of brood defence in the great tit *Parus major* L. Behav Ecol Sociobiol 13:131-145
- Reid ML, Montgomerie RD (1985) Seasonal patterns of nest defence by Baird's sandpipers. Can J Zool 63:2207-2211
- Ricklefs R (1969) An analysis of nesting mortality in birds. Smithson Contr Zool 9:1-48
- Robertson RJ, Biermann GC (1979) Parental investment strategies determined by expected benefits. Z Tierpsychol 50:124-128
- Röell A, Bossema I (1982) A comparison of nest defence by jackdaws, rooks, magpies and crows. Behav Ecol Sociobiol 11:1–6
- Schaller GB, Emlen JT (1961) The development of visual discrimination patterns in the crouching reactions of nestling grackles. Auk 78:125–137
- Shalter MD (1979) Responses of nesting passerines to alarm calls. Ibis 121:362–368
- Skutch AF (1976) Parent birds and their young. Univ Texas Press, Austin
- Stephens ML (1984) Interspecific aggressive behavior of the polyandrous northern jacana (Jacana spinosa). Auk 101:508-518
- Tatner P (1982) The breeding biology of magpies *Pica pica* in an urban environment. J Zool London 197:559–581
- Tiainen J (1983a) Ecological energetics of nestling growth in the willow warbler *Phylloscopus trochilus*. Annu Zool Fennici 20:13–24
- Tiainen J (1983 b) Dynamics of a local population of the willow warbler *Phylloscopus trochilus* in southern Finland, Ornis Scand 14:1-15
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, pp 136–179
- Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249-264
- Verbeek NAM (1973) The exploitation system of the yellowbilled magpie. Univ Calif Publ Zool 99:1–58
- Weatherhead RJ (1979) Do savannah sparrows commit the Concorde fallacy? Behav Ecol Sociobiol 5:373-381
- Werschkul DF (1979) Nestling mortality and the adaptive significance of early locomotion in the little blue heron. Auk 96:115-130
- Willis EO (1973) Survival rates of visited and unvisited nests of bicolored antbirds. Auk 90:263-267
- Woodall PF (1973) On the life history of the bronze mannikin. Ostrich 46:55–86
- Young H (1963) Age-specific mortality in the eggs and nestlings of blackbirds. Auk 80:145–155