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ACTIVITY, SURVIVAL, INDEPENDENCE AND MIGRATION OF FLEDGLING GREAT SPOTTED CUCKOOS[1]

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Parental care of fledglings tends to last at least as long as that of nestlings, and in some cases twice as long (Skutch 1976). The post-fledging dependence period (hereafter called fledgling period) is critical for juvenile survival (Royama 1966, Sullivan 1989), and the probability of survival to independence appears to be an adequate estimate of relative probabilities of survival to breeding in many bird species (Magrath 1991).

For avian brood parasites, very little is known about the behavior of foster parents in relation to their fledgling parasites (see review in Payne 1977 and Rothstein 1990). Only one detailed study exists (Woodward 1983), namely, on the fledging period of the Brown-headed Cowbird, *Molothrus ater.* Cowbirds are conspicuous after they leave the nest (Woodward 1983), in contrast to other fledgling parasites such as European Cuckoos, *Cuculus canorus,* which hide in the vegetation and remain immobile for long periods of time (Wyllie 1981).

The Great Spotted Cuckoo *Clamator glandarius* is an obligate brood parasite which in Europe mainly parasitizes magpies *Pica pica* (Cramp 1985). We have shown that Great Spotted Cuckoo fledglings often formed flocks (group size ranged from one to five), and that every group of cuckoo fledglings was attended by a group of magpies (Soler et al., unpubl. manuscript). Cuckoo fledgling groups were frequently attended by more magpies than those involved in nestling rearing, and the feeding rate of fledgling cuckoos increased with the number of cuckoos per group and the number of adult magpies attending the group of fledgling cuckoos.

We studied the behavior of fledgling Great Spotted Cuckoos. We paid special attention to the following aspects: (1) changes in the activity of fledgling cuckoos with age, (2) survival of fledgling cuckoos and magpies in parasitized nests, (3) post-fledgling dependence, and (4) migration of fledgling and adult cuckoos.

MATERIAL AND METHODS

Field work was carried out in Hoya de Guadix, southern Spain (37°10′N, 3°11′W), a cereal-producing plateau that is approximately 1,000 m a.s.l. A detailed description of the study site is given in Soler (1990) and Soler et al. (in press).

In all nests found, chicks were banded with numbered aluminium rings (Spanish Institute for Nature Conservation—ICONA). In 1991, a total of 19 Great Spotted Cuckoo chicks reared in 13 parasitized magpie nests were fitted with radiotransmitters. In 1992, 21 cuckoo chicks and four magpie chicks were radio-tagged. In 1992, only one cuckoo chick in each nest was provided with a radiotransmitter and all were weighed with a 300 g Pesola spring balance one or two days before they left the nest. Other cuckoo chicks in these nests were given a unique combination of color bands to enable individual recognition. To facilitate identification, we attached a color tag (8 cm) of nylon coated vinyl (Saflags) on each color ring.

One or two days before leaving the nest (when 15 days old), 44 chicks were fitted with radiotransmitters weighing approximately 4 g each (back-pack harness included), with a trailing 20 cm wire antenna (Biotrack, Dorset, UK). Transmitters had a range up to 1,000 m and a lifespan of 10–12 weeks.

This study was conducted throughout the breeding seasons of 1991 and 1992. A total of 111 and 166 magpie nests was studied in 1991 and 1992, of which 58.6% and 66.9%, respectively, were parasitized by the Great Spotted Cuckoo. Nests were inspected at least once a week, and parasitized nests two, three or four times a week.

Fledglings often remained well-hidden in the tree canopy. We therefore had at least one radio-tagged cuckoo chick in every group. We used the radio-tracking method only to locate the trees occupied by the radio-tagged chicks. Between 25 May and 8 August in both 1991 and 1992, systematic observations were made. Each group was located at least two or three times per week and, when the fledglings were present in an open and easily visible area, each fledgling was watched for 0.5–3 hr.

A total of 104 hr of effective observation was recorded in 1991 and 164 hr in 1992. We observed parental feedings and the behavior of young from a distance of 20–100 m (mostly 40–50 m, and from the cover of a car whenever possible) with binoculars (10×). The following data were recorded: individual, time of day, location, whether the fledgling was on the ground or perching in a tree, whether the bird was flying alone or following one of the foster parents, and what the

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TABLE 1. Survival and mass of Great Spotted Cuckoo fledglings.

	1991		1992		Mass (g)
	n	%	*n*	%	($\bar{x}$ ± SD)
Survived until independence	11	64.7	13	61.9	138 ± 8.31
Failed to survive	6	35.3	8	38.1	124 ± 10.82
Depredated	5	29.4	5	23.8	130 ± 4.27
Starved	1	5.9	3	14.3	115 ± 13.32
Total	17	100.0	21	100.0	133 ± 11.52

fledgling was fed by an adult magpie. The age of the young was expressed as days after leaving the nest, with day 1 being the first day after leaving the nest.

Relationships between behavioral parameters of groups of fledgling cuckoos and parameters of attending magpies were analyzed by, first calculating the correlation coefficients (r) for each group separately, which values were z-transformed (Sokal and Rohlf 1981), and then, testing if they differed from 0 in a one-sample t-test. When analyses involved fledglings they were made in the same way, but we used only one fledgling per group (the radio-tagged fledgling which is the one with greater number of observations), because the behavior of fledglings in each group is not independent.

RESULTS

Age-related changes in cuckoo activity. During the first three days out of the nest, Great Spotted Cuckoo fledglings perched quietly in the vicinity of the nest, well hidden in the tree canopy, except when magpies came to the area with food. After these three days, fledging cuckoos become more active, moving on their perches and flying around more frequently. Later, the young chased the magpies actively while begging for food. Cuckoo groups were very sedentary, they usually occupied the same area over the season.

The number of flights per hour did not increase with age (mean $r = -0.07$, H_0: $r = 0$, $t = 0.3$, $P = 0.77$), and the number of times that fledglings flew to the ground did not increase as the fledglings aged. Time spent on the ground did not vary with age either; contrary to expectation, we found a slight decrease with age (mean $r = -0.18$, H_0: $r = 0$, $t = 0.79$, $P = 0.49$).

Unexpectedly fledgling cuckoos did not feed themselves. In 268 hr of effective observation, we only occasionally saw a fledgling cuckoo pecking at objects on the ground, but never saw self-feeding.

Fledgling survival. Out of a total of 38 fledgling cuckoos fitted with radiotransmitters, 24 (63.2%) survived to independence and 14 (36.8%) died, either from predation (26.3%) or starvation (10.5%). Results were similar in both study years (Table 1). Great Spotted Cuckoos that died after fledging weighed significantly less when ringed than those which survived to independence (Table 1, Mann-Whitney U-test, $U = 13.5$, $P = 0.004$). Those which were starved did not weigh significantly different from those which were preyed upon (Table 1, Mann-Whitney U-test, $U = 5.5$, $P = 0.27$).

In three parasitized magpie nests where both cuckoo and magpie chicks fledged, four magpie chicks were fitted with radiotransmitters. Two of these chicks starved, four and six days, respectively, after leaving the nest. The other two were killed by predators four and twelve days, respectively, after leaving the nest.

Independence and migration. Adult Great Spotted Cuckoos left the study area in mid-June in both years, disappearing over a few days. The last adult cuckoo was seen on 17 June 1991 and 18 June 1992.

Post-fledging dependence of Great Spotted Cuckoo fledglings ranged from 25 to 59 days ($\bar{x} = 33.2$, SD = 11.63, $n = 25$). This large variation is due to every fledgling cuckoo being fed until the moment in which all of them left the area. Thus, the sooner a cuckoo chick leaves the nest, the more prolonged is the period during which it is attended by magpies.

In 1991, all the six groups of fledglings left the breeding area between 9 July and 8 August. In 1992 two groups disappeared considerably sooner, between 5 and 12 June. The other 11 groups left the area at about the same time as in 1991. When a fledgling group disappeared from the home area, we looked for the radio-tagged birds in a more extensive area (approximately 5 km diameter), and if no birds were found the group was considered to have migrated. Usually the fledglings left suddenly and directly. Only on one occasion was a group which had disappeared from the home area found again, at a distance of 2.3 km. This group remained at this second site for 5 days and then disappeared again.

The last adult cuckoo was seen in the study area on 17 June in 1991 and on 18 June in 1992. Thus, it can be concluded that fledgling and adult cuckoos do not migrate together, adults leaving the breeding area about two months earlier than the majority of the juveniles.

DISCUSSION

Age-related changes in activity. Davies (1976, 1978) showed that parental reluctance to feed the young forces them to become more independent. This observation has been supported in most species where fledgling behavior has been studied (Holleback 1974, Moreno 1984, Buitron 1988, Husby and Slagsvold 1992). However, it has been suggested that the dependence period is determined by the young in some raptor species where the migratory departure of young affect the post-fledging dependence period (Bustamante and Hiraldo 1990, Ferrer 1992).

In Brown-headed Cowbird fledglings, activity was also found to increase with age. It is likely that the host parents force the young to feed themselves by becoming more reluctant and finally by refusing to provide food

(Woodward 1983). However, this was not the case with Great Spotted Cuckoo fledglings, for which time spent in self-feeding did not increase and time spent begging did not decrease; indeed, the provisioning rate of each fledgling cuckoo tended to increase with age (Soler et al., unpubl. manuscript).

According to Norton-Griffiths (1969), these changes have two components: the first is a motivational change leading to a reduction in the parents' feeding behavior, and the second is dependent on how intensively and for how long the young demand food. Fledgling cuckoos begged loudly and persistently throughout the fledgling period; however, a similar behavior has been found in the parasitic fledgling Brown-headed Cowbirds (Woodward 1983), even though their host stopped feeding them. The intensive begging behavior of fledgling magpies from unparasitized broods elicited no reaction from their parents after days 51–55 (Husby and Slagsvold 1992).

Why did magpies not reduce parental care when they were rearing cuckoos? This is discussed in detail by Soler et al. (unpubl. manuscript), in which three nonexclusive hypotheses are proposed. (1) The fledgling cuckoo may be a supernormal releaser for parental care. (2) Adult magpies attending fledgling cuckoos in the groups were displaying their ability as good parents which might increase their possibilities to obtain a mate and/or a territory. (3) Parental care provided by magpies other than the foster parents could be an unselected consequence of the fact that they are exposed to the begging fledglings.

Fledging survival, independence and migration. The survival rate of Great Spotted Cuckoo chicks to independence (63.2%) is high, considering that in unparasitized magpie nests an overall mortality rate of 50% between the end of the nestling period and independence has been recorded (Husby and Slagsvold 1992). Survival rate has also been found to be very high in the European Cuckoo, where 32 of 38 wing-tagged young reached independence (Wyllie 1981).

Martin (1987) stated that large and heavy nestlings enjoy a higher probability juvenile survival. This assertion has been supported in some studies, but its general validity remains to be demonstrated (reviewed by Magrath [1991], but see Lindén et al. [1992] for conflicting evidence). We have found a strong positive relationship between nestling weight and juvenile survival. In unparasitized magpie nests, it has also been found that smaller nestlings suffer a higher rate of post-fledgling mortality as compared to larger ones (Husby and Slagsvold 1992).

The post-fledgling dependence period of Great Spotted Cuckoo fledglings is unusually long (in some cases more than 50 days). This period lasts about 20 days for fledgling magpies (Husby and Slagsvold 1992). In the European Cuckoo it is as short as in non-parasitic species of the same size, young parasites remaining dependent on the hosts after fledging for two to three weeks (Wyllie 1981). However, a long post-fledgling dependence period seems to be the rule in *Clamator* species, given that it has been recorded that Striped Cuckoo (*Clamator levaillantii*) fledglings were fed by their foster parents for at least 36 days after leaving the nest (Steyn 1973). Why is there such a long post-fledgling dependence period in the Great Spotted Cuckoo? We suggest the primary reason to be ecological constraints related to food availability. Cuckoos in general have a specialized diet based on gregarious hairy caterpillars, which in our study area are not available after June (Soler et al., unpubl. data). At this time of the year and later, the only abundant prey are beetles and grasshoppers, which may not be easy to catch for juvenile cuckoos. Therefore, the best survival prospect for fledglings may be to prolong feeding by the host in order to store the fat necessary for migration. Our observations suggest that young cuckoos leave on migration without having learned to forage by being totally reliant on magpie foster parents. In the European Cuckoo, the post-fledgling dependence period is considerably shorter, probably because adequate prey are available for juvenile European Cuckoos. This argument is supported by the fact that adult Great Spotted Cuckoos migrate in mid-June, whereas adult European Cuckoo migration through Europe lasts from late June to October (Wyllie 1981).

Adult Great Spotted Cuckoos migrate earlier than juveniles. In the European Cuckoo it has also been recorded that southward autumn migrations begin earlier in adults than in juveniles (Wyllie 1981). This means that young cuckoo migrants are able to find their wintering area without the help of conspecifics, suggesting a genetic basis to this behavior, as has been demonstrated in the Blackcap *Sylvia atricapilla* (Berthold and Quermer 1981, Helbig 1991).

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LITERATURE CITED

BERTHOLD, P., AND U. QUERMER. 1981. Genetic basis of migratory behaviour in European warblers. Science 212:77–79.

BUITRON, D. 1988. Female and male specialization in parental care and its consequences in Black-billed Magpies. Condor 90:29–39.

BUSTAMANTE, J., AND F. HIRALDO 1990. Factors influencing family rupture and parent-offspring conflict in the Black Kite *Milvus migrans.* Ibis 132: 58–67.

CRAMP, S. [ED.]. 1985. The birds of the Western Palearctic, Vol. IV. Oxford University Press, Oxford, U. K.

DAVIES, N. B. 1976. Parental care and the transition to independent feeding in the young Spotted Flycatcher (*Muscicapa striata*). Behaviour 59:280–295.

DAVIES, N. B. 1978. Parental meanness and offspring independence: an experiment with hand-reared Great Tits *Parus major.* Ibis 120:509–514.

FERRER, M. 1992. Regulation of the period of post-fledging dependence in the Spanish Imperial Eagle *Aquila adalberti.* Ibis 134:128–133.

HELBIG, A. J. 1991. Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating Blackcaps (*Sylvia atricapilla*). Behav. Ecol. Sociobiol. 28:9–12.

HOLLEBACK, M. 1974. Behavioral interactions and the dispersal of the family in Black-capped Chickadees. Wilson Bull. 86:466–468.

HUSBY, M., AND T. SLAGSVOLD. 1992. Post-fledgling behaviour and survival in male and female magpies *Pica pica*. Ornis Scand. 23:483–490.

LINDÉN, M., L. GUSTAFSSON, AND T. PÄRT. 1992. Selection on fledging mass in the Collared Flycatcher and the Great Tit. Ecology 73:336–343.

MAGRATH, R. D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. J. Anim. Ecol. 60:335–351.

MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annu. Rev. Ecol. Syst. 18:453–487.

MORENO, J. 1984. Parental care of fledged young, division of labor, and the development of foraging techniques in the Northern Wheatear (*Oenanthe oenanthe* L.). Auk 101:741–752.

NORTON-GRIFFITHS, M. 1969. The organization, control and development of parental feeding in the Oystercatcher (*Haematopus ostralegus*). Behaviour 34:55–114.

PAYNE, R. B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8:1–28.

ROTHSTEIN, S. I. 1990. A model system for coevolution: avian brood parasitism. Ann. Rev. Ecol. Syst. 21:481–508.

ROYAMA, T. 1966. Factors governing feeding rate, food requirements and brood size of nestling Great Tit *Parus major*. Ibis 108:313–347.

SKUTCH, A. F. 1976. Parent birds and their young. Univ. Texas Press, Austin, TX.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd edn. W. H. Freeman, New York.

SOLER, M. 1990. Relationship between the Great Spotted Cuckoo, *Clamator glandarius*, and its corvid hosts in a recently colonized area. Ornis Scand. 21:212–223.

SOLER, M., AND J. J. SOLER. 1991. Growth and development of the Great Spotted Cuckoos and their magpie host. Condor 93:49–54.

SOLER, M., J. J. SOLER, AND J. G. MARTINEZ. In press. Sympatry and coevolution between the Great Spotted Cuckoo (*Clamator glandarius*) and its magpie (*Pica pica*) host. *In* S. I. Rothstein [ed.], Evolution and ecology of brood parasitism.

STEYN, P. 1973. Some notes on the breeding biology of the Striped Cuckoo. Ostrich 44:163–169.

SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). J. Anim. Ecol. 58:275–286.

WOODWARD, P. W. 1983. Behavioral ecology of fledgling Brown-headed Cowbirds and their hosts. Condor 85:151–163.

WYLLIE, J. 1981. The cuckoo. B. Y. Batsford, London.

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A TECHNIQUE FOR MEASURING PRECOCIAL CHICKS FROM PHOTOGRAPHS[1]

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Key words: *American Coot;* Fulica americana; *body size; distance; growth rate; nidifugous chicks; photography.*

Measures of the body size and growth rate of chicks are central to many avian studies (Ricklefs 1983). In some species, growth rate or body size at fledging is correlated with subsequent recruitment into the population (Perrins 1965), indicating that these measures can be important indices of fitness. In nidicolous birds, measures of nestling body size can be obtained simply by visiting nests. However, obtaining growth data for the nidifugous young of precocial birds is often far more difficult. Here I describe a technique for estimating the size of objects in photographs and show how this technique can be used to obtain size and growth measures for chicks, especially the swimming chicks of aquatic species that can be approached with floating blinds (Nuechterlein 1982). I then demonstrate the accuracy and utility of this method using data collected from both captive and free-ranging American Coot (*Fulica americana*) chicks.

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