

Food acquisition by common cuckoo chicks in rufous bush robin nests and the advantage of eviction behaviour

DAVID MARTÍN-GÁLVEZ*, MANUEL SOLER†, JUAN JOSÉ SOLER*, MANUEL MARTÍN-VIVALDI† & JOSÉ JAVIER PALOMINO†

*Estación Experimental de Zonas Áridas (C.S.I.C.)

†Departamento de Biología Animal y Ecología, Universidad de Granada

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The common cuckoo, *Cuculus canorus*, is a brood parasite that monopolizes parental care of its host species: soon after hatching, the chicks remove the host offspring. Although cuckoo chicks trick their foster parents into providing enough food, it is unknown whether cuckoo begging behaviour represents an advantage over that of the host chicks in a hypothetical competitive scenario. We studied the feeding behaviour of rufous bush robins, *Cercotrichas galactotes*, when rearing their own and parasitic chicks in natural and in experimental nests where a cuckoo and a host brood were presented simultaneously to parents. In natural parasitized and nonparasitized nests, the feeding rate for cuckoo chicks did not differ from that of a single host chick of the same age, but cuckoos were fed with a different diet and with larger prey. Thus, cuckoo chicks received a similar amount of food to that received by a whole host brood. Cuckoo chicks in experimental nests did not receive a diet, prey size or feeding rate different to that received by a single host chick and thus received considerably less food than cuckoo chicks in unmanipulated nests. These results suggest that cuckoo chicks could not outcompete host chicks, at least when parasitizing this host species, and thus that their eviction behaviour is beneficial. We discuss various explanations for the inability of cuckoos to outcompete host chicks.

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Brood parasitism is a reproductive strategy in which certain individuals, the parasites, receive parental care from unrelated individuals, the hosts (Rothstein 1990). The common cuckoo, *Cuculus canorus*, is an obligate brood parasite which parasitizes about a hundred species in Europe, mainly small and abundant passerines with open nests and short nestling periods (Soler et al. 1999), although the frequency of parasitism varies between species (Wyllie 1981; Moksnes & Røskaft 1995). The common cuckoo female lays one egg per host nest, but usually removes and eats one of the host's eggs. In general, the cuckoo egg hatches before those of the host and, in a few hours (8–36), cuckoo chicks start evicting host offspring from the nest (hereafter eviction behaviour)

Correspondence: D. Martín-Gálvez, Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (C.S.I.C.), C/General Segura, 1, E-04001-Almería, Spain (email: dmartin@eeza.csic.es). M. Soler, M. Martín-Vivaldi & J. J. Palomino are at the Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada. Campus de Fuentenueva, s/n, E-18071, Granada, Spain.

without any host parent obstruction, thereby remaining alone in the host nest. This urge to eject nest contents dissipates after 4 days (Wyllie 1981).

Eviction behaviour is likely to be costly, because of the great relative weight that the cuckoo chick has to move in a short time at a considerable height, and because of the risk of falling from the nest while trying to eject foster siblings (Wyllie 1981). Kleven et al. (1999) provided an indirect measure of such costs: they found that although the increase in weight of cuckoo chicks reared by reed warblers, *Acrocephalus scirpaceus*, was generally lower than that of chicks reared by great reed warblers, *Acrocephalus arundinaceus*, the opposite occurred during the first 3 days of the nestling period. Kleven et al. suggested that the larger eggs and deeper nests of great reed warblers increased the energy cost associated with the ejection behaviour.

It is generally assumed that the high begging rate and large gape of the cuckoo chick, compared with those of a host chick (Kilner & Davies 1999; Kilner et al. 1999), trick the foster parents into increasing their feeding effort up to the level needed for its normal development (Davies 2000). Several mechanisms have been proposed to explain

how such exaggerated cues would affect parental effort. (1) A cuckoo chick may imitate the begging signals of a complete host brood (Davies et al. 1998). (2) A cuckoo chick may compensate for its deficient visual cue (only one gape) by exaggerating its call rate, through tuning into the sensory predispositions of the adult host (Kilner & Davies 1999; Kilner et al. 1999). (3) A cuckoo chick could also be a supernormal stimulus, which would prevent its recognition as a parasitic chick by adult hosts despite its odd appearance (Dawkins & Krebs 1979; Redondo 1993). Finally, (4) the exaggerated begging behaviour of a cuckoo chick could merely indicate its greater need compared to the need of a single host chick (Soler & Soler 1999; Grim & Honza 2001) and thus exploit the honest signalling system between chicks and parents.

If the exaggerated feeding behaviour of foster parents towards a single cuckoo chick is related to the higher begging intensity of cuckoos (reviewed in Kilner & Johnstone 1997), parasitic chicks should be able to outcompete host chicks if they shared the nest with foster siblings. This is the case for chicks of some nonevictor parasites (e.g. brown-headed cowbird, *Molothrus ater*: Dearborn 1998; Lichtenstein & Sealy 1998; some Cuculidae species: Davies 2000). Furthermore, cuckoo chicks could even benefit from assistance by host chicks in soliciting a higher provisioning rate (Kilner 2003). Taking into account both the high energetic costs associated with the eviction behaviour (see above) and the ability of cuckoo chicks to trick their foster parents, an important evolutionary question arises: what advantage does eviction behaviour confer on cuckoo chicks? The answer to this question could be related to an inability of cuckoo chicks to stimulate foster parents to feed them preferentially in a hypothetical competitive scenario with host chicks.

To test this hypothesis, we examined the feeding behaviour of the rufous bush robin, *Cercotrichas galactotes*, a small passerine (ca. 23 g) frequently used as a host by the common cuckoo in southern Iberia (Alvarez 1994a; Palomino et al. 1999), in natural and experimental nests where cuckoo and host chicks were presented together to adults. Since the increase in weight of a brood of rufous bush robins does not differ from that of a single cuckoo chick (Alvarez 1994b), relative food provisioning to cuckoos and complete host broods should be similar in parasitized and nonparasitized natural nests (Wyllie 1981; Kilner & Davies 1999). However, if cuckoo chicks were not able to outcompete host siblings in a hypothetical competitive scenario, cuckoo chicks in experimental nests should receive less food than in naturally parasitized nests.

METHODS

Study Area and General Field Procedures

We carried out the fieldwork during 1994–1995 in a wine-growing region in Los Palacios, southern Spain (37°9'N, 2°14'W; 12 m above sea level). The study area comprised vineyards with scattered fruit trees, and with small patches used for vegetable production. Rufous bush robins show a marked preference for breeding in

these vineyards. This region has a Mediterranean climate, with rainy autumns and springs, and hot, dry summers.

We found nests by following the breeding activities of pairs and looking in suitable nest sites, mainly in vineyards. We checked all nests twice a week during incubation and every 2 days during the nestling period to collect data on laying date, clutch size, presence or absence of brood parasitism, number of hatched eggs and number of fledglings. Rufous bush robin and cuckoo chicks were weighed at 9 and 15 days, respectively. Subsequently, they were ringed (under licences from the Consejería de Medio Ambiente de la Junta de Andalucía) with a numbered aluminium ring and a colour ring (different every year).

Video Recordings

The nests were videorecorded to estimate feeding variables. In total, we recorded 25 pairs: four unmanipulated parasitized pairs (cuckoo chick alone); 10 unmanipulated nonparasitized pairs (two with four rufous bush robin chicks and eight with three); and 11 experimental pairs (one with three rufous bush robin chicks and one cuckoo chick, and 10 with two rufous bush robin chicks and one cuckoo chick). Because excluding the experimental nest with three host chicks did not change the results, we included this nest in the analyses. Eight of the 11 experimental pairs were previously not parasitized, whereas three of them were. Host chicks were 5–9 days old ($\bar{X} \pm \text{SD} = 7.10 \pm 1.3$ days) and cuckoo chicks 5–10 days old (7.20 ± 1.57 days). Differences in age between experimental rufous bush robin and experimental cuckoo chicks varied between 0 and 4 days: for five experimental pairs there was no difference between host and cuckoo chicks; for two pairs host chicks were older than cuckoo chicks; and in four pairs cuckoo chicks were older than host chicks.

All nonexperimental nests were recorded only once. However, for recording the 11 experimental pairs, we used only seven cuckoo chicks in 11 host nests, mainly because we found too few cuckoo chicks of the right age. Although reusing chicks could be seen as a pseudoreplication problem, we did not find significant differences associated with cuckoo chick identity for any feeding variable (see below), even after controlling for age (one-way ANCOVA with age as covariate: provisioning rate: $F_{6,3} = 1.77$, $P = 0.342$; prey size: $F_{6,3} = 1.42$, $P = 0.416$; amount of food: $F_{6,3} = 2.20$, $P = 0.276$). Whether chicks had experience of sharing parental care with foster siblings did not affect our results since residuals of provisioning rate, or amount of food received, after we controlled for age did not vary between experimental cuckoos with and without experience (t test: provisioning rate: $t_9 = -0.34$, $P = 0.737$; amount of food: $t_9 = -0.46$, $P = 0.653$). Thus, because feeding variables were mainly related to foster parents, and not to individual cuckoo characteristics, the use of some cuckoo chicks in more than one experimental nest did not affect our results.

We videorecorded unmanipulated nests for 2–2.5 h and experimental nests for about 4 h, divided into two sessions of 2 h (see below). All recordings were started between 0700 and 0930 hours (local time), except for one unmanipulated

parasitized nest for which recording started at 1600 hours (excluding this late-filmed nest from the analyses did not change our results, although the significant differences in provisioning rate found between cuckoo chick and unmanipulated host brood (see below) become marginally significant, from 0.035 to 0.08). The video camera was installed 0.5–1 m from the nests.

To carry out the experiment, we placed cuckoo and host chicks into two separate nests (i.e. one additional nest close to the natural nest), thereby preventing the cuckoo from evicting the rufous bush robin chicks (see Davies & Brooke 1988, for a similar experimental design). A single nest also does not provide sufficient space for one cuckoo chick plus two or three host chicks. Additional nests were empty nests collected in the same area that had suffered from natural predation. We placed the additional nest close to and at the same height as the natural nest. Since naturally parasitized pairs always rear a single cuckoo chick, our experimental approach required us to use chicks from two pairs for each recording, one parasitized and one nonparasitized (Fig. 1). To avoid nest desertion during the experiment, when we used a nonparasitized pair for video recording (Fig. 1a), we cross-fostered one host chick from this pair to the experimental cuckoo chick nest and thus the rufous bush robin chick was fed by the pair not used in the video recording. When we recorded a naturally parasitized pair (Fig. 1b), we used all but one host chicks from the nonparasitized pair. By using the host brood minus one chick, we imitated a rufous bush robin brood parasitized by a nonevictor cuckoo chick where the cuckoo female had removed a host egg. Thus, the experimental scenario was one cuckoo chick in one randomly chosen nest and the rufous bush robin brood minus one host chick in the other nest. At mid-recording time (2 h), the contents of each nest were exchanged to control for possible effects of position.

The adults seemed not to be disturbed by the presence of the recording material or by the additional nest, and resumed normal activity within a few minutes. When the recordings were finished, chicks were returned to their original nests.

Ethical Note

The population studied is concentrated in an agricultural area. The vineyards were frequently visited by the farmers (more than two visits per week, in some cases daily) in the breeding season so our study pairs were used to human disturbance. Moving chicks between nests took about 0.5–1 h and the high ambient temperatures (mean daytime air temperature of around 27°C) meant that chicks did not require additional warming during transport or while they were in the additional nests.

To assess possible negative impacts of our manipulations on chicks and pairs, we compared mean body mass of host chicks and brood size at 9 days old, just before fledging. We used only host chicks because most cuckoo chicks were recorded and thus manipulated. The average weight did not differ between host chicks from filmed (19.30 ± 1.89 g, $N = 17$ pairs) and nonfilmed (18.99 ± 3.71 g, $N = 42$ pairs) broods (one-way ANCOVA with number of successful fledglings as covariate: $F_{1,59} = 0.17$, $P = 0.685$). Number of successful fledglings did not differ between filmed and nonfilmed broods (filmed broods: 3.12 ± 0.49 ; nonfilmed broods: 2.79 ± 0.80 ; one-way ANOVA: $F_{1,60} = 2.50$, $P = 0.119$). In addition, we did not find any differences in average body mass of host chicks between experimental broods (whose nest contents were rearranged and transferred; 18.97 ± 2.05 g, $N = 7$), control broods (whose nest contents were only recorded; 19.53 ± 1.84 g, $N = 10$) and nonrecorded broods (18.99 ± 3.7 g, $N = 42$; one-way ANCOVA with number of successful fledglings as covariate: $F_{2,58} = 0.15$, $P = 0.861$; all post hoc comparisons NS). Finally, differences in fledging success between these three groups of nests were not statistically significant (experimental broods: 3.00 ± 0.58 ; control broods: 3.20 ± 0.42 ; nonfilmed broods: 3.12 ± 0.49 ; one-way ANOVA: $F_{2,59} = 1.39$, $P = 0.258$; all post hoc comparisons NS). Therefore, no negative effects on nestlings were detected in this study as a consequence of our manipulations.

Fieldwork was done with special permission of the Andalusia government (Consejería de Medio Ambiente de la Junta de Andalucía).

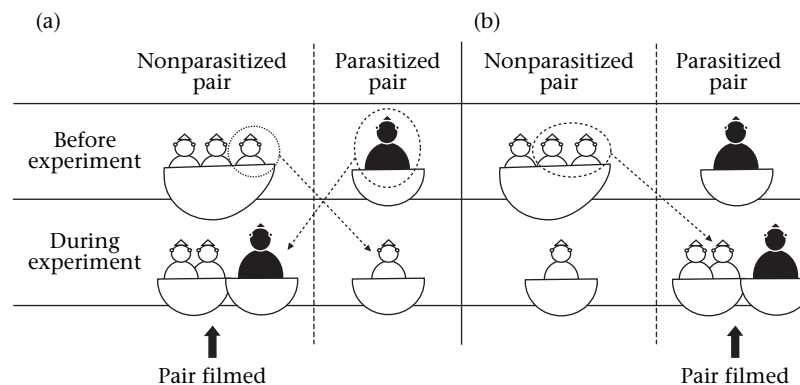


Figure 1. Diagram showing how experimental chicks were moved between nests. When we recorded the nonparasitized pair (a), one host chick (white chick symbol) replaced the cuckoo chick (black chick symbol) in the parasitized pair. In contrast, when we filmed the parasitized pair (b), all but one of the host chicks were moved to the parasitized experimental pair's nest.

Analyses

We obtained the following data from each recording: total duration; time between feeding trips; number of chicks that begged for per adult feeding visit; type of prey carried (larva, grasshopper, etc., when distinguishable; Table 1); size of prey relative to adult bill length (1: smaller; 2: similar; 3: larger); and the chick chosen to be fed. The same person made all prey determinations. Because it was difficult to identify small prey (determined versus undetermined prey size: 1.99 ± 0.77 ($N = 485$) versus 1.35 ± 0.52 ($N = 222$); t test: $t_{705} = -11.27$, $P < 0.001$) a large number of food items were included in an undetermined category. However, since prey size is taxon dependent we included this prey category in the analysis of differences in diets of cuckoo and host chicks.

Provisioning rate was estimated as the number of prey brought to the nests per hour from the first to the last feeding trip recorded. Since we visited experimental nests to change chick positions, we estimated values of provisioning rate (as well as other variables) separately for each of the two recording sessions. We used number of prey brought to the nests instead of the number of feeding trips because on some occasions the adults carried more than one prey (usually two or three, occasionally even four) to the nest in a single trip (multiple feedings). Multiple feedings occurred mainly in natural nonparasitized nests (nonparasitized: 9.47%; parasitized: 0%) and in experimental nests (3.08%). When multiple feeding occurred, prey were smaller than when adults carried a single prey (multiple feedings: 1.47 ± 0.65 ($N = 91$); single

feedings: 1.82 ± 0.76 ($N = 574$); t test: $t_{663} = -4.48$, $P < 0.001$) and, thus, we used number of prey together with prey size in the analyses related to parental effort. We calculated the total amount of food carried to the nest per hour by multiplying the provisioning rate by average prey size. We estimated diet by considering the total number of prey received per nest and per chick species. Then, we estimated relative percentages of each prey type per nest in unmanipulated nests or per nest and species of chick in experimental nests. Afterwards, we determined the average of the relative percentages of each prey type received by cuckoo and rufous bush robin chicks in both the unmanipulated nests and the experimental nests (Table 1).

Statistical Procedures

Distributions of most feeding variables did not differ significantly from normal distributions (Kolmogorov–Smirnov test: NS). Therefore, for these variables we used parametric tests following Sokal & Rohlf (1995). We used a nonparametric analysis when distributions of variables differed significantly from normal distributions (Kolmogorov–Smirnov test: $P < 0.05$). We used a chi-square test to compare the diets of cuckoo and rufous bush robin chicks provided by both unmanipulated and experimental pairs. Expected frequencies in this last analysis were the average of the observed frequencies for cuckoo and rufous bush robin chicks and, thus, either of the two diets (cuckoo or rufous bush robin) can be used in the analysis as observed frequencies (Table 1).

We used one-way ANCOVA with nestling age as covariate to test for differences in feeding variables (provisioning rate, prey size and the total amount of food) between unmanipulated parasitized and unmanipulated nonparasitized pairs, thereby controlling for differences in chick age, which could affect feeding variables. We also used this analysis to compare the amount of food delivered by the different types of rufous bush robin pairs (i.e. experimental, unmanipulated nonparasitized and unmanipulated parasitized pairs). Instead, to evaluate the amount of food delivered per chick by unmanipulated and experimental pairs, we used two-way ANCOVA with chick age as covariate, species as one between-groups factor and experimental or nonexperimental status as the second between-groups factor. Post hoc least significant difference (LSD) tests were used to contrast groups within an analysis.

To test for differences in feeding variables between cuckoo and rufous bush robin chicks in the experimental nests, we used repeated measures ANOVAs with two within-group factors: original or additional nests and chick species. Nest parasitism status (i.e. parasitized or nonparasitized before the experiment) was included as a between-groups factor and the difference in age between cuckoo and host chicks (age of cuckoo chicks minus age of host chicks) as covariate. Thus, this analytical design has the advantages of controlling for possible differences in feeding behaviour between experimental pairs (i.e. paired

Table 1. Average percentages of each prey type received by rufous bush robin and cuckoo chicks in unmanipulated and experimental nests

Prey type	% In unmanipulated nests		% In experimental nests	
	Cuckoo chicks	Host broods	Cuckoo chicks	Host broods
Larvae	51.87	36.00	51.32	41.83
Arachnida	2.08	0.74	0.40*	1.00
Diptera	0*	0.17	0	0
Neuroptera	0*	0.28	2.52	4.18
Odonata	0*	0.40	0	0
Dermoptera	0*	0.48	0.00*	0.57
Orthoptera: Caelifera	1.47	7.59	4.10	4.01
Orthoptera: Ensifera	0	2.10	7.06	6.15
Lepidoptera	0*	1.83	2.27	0.89
Homoptera	1.47*	0.17	0	0
Heteroptera	0	2.95	0	0
Pupae	0*	0.72	0.00*	1.14
Hymenoptera	0	2.35	2.60	0.94
Coleoptera	6.33	1.41	0.00	2.31
Chilopoda	0*	0.17	0	0
Diplopoda	0*	1.67	0	0
Grape	16.89	3.74	0.40	2.75
Undetermined	19.89	37.24	29.34	34.22

*Prey type included within a category 'others' for statistical analyses when the average percentage for both cuckoo chicks and host broods was below 2%.

tests) and of allowing us to explore the interactions between different factors included in the model.

This statistical design was also used for testing whether the begging signal of one species was chosen preferentially in experimental nests (repeated measures ANOVAs with nest parasitism status as a between-groups factor and age differences as covariate). In this case, the repeated measures were the percentage of feeds received by one chick species when the other one was or was not begging as one within-group factor, and the original or additional nest as the second one.

For all statistical analyses we used STATISTICA version 6.0 (Statsoft Inc., www.statsoft.com) and all tests were two tailed. Values are means \pm SD.

RESULTS

Feeding in Natural Conditions

Provisioning rate to cuckoos in naturally parasitized nests was on average less than a half of that to host broods in nonparasitized nests (nonparasitized: 16.97 ± 8.21 prey/h; parasitized: 6.45 ± 2.10 prey/h; one-way ANCOVA with nestling age as covariate: $F_{1,11} = 5.76$, $P = 0.035$). However, parasitized pairs provided cuckoo chicks with larger prey than nonparasitized pairs gave to their own young (cuckoo chicks: 2.15 ± 0.18 ; host broods: 1.65 ± 0.28 ; one-way ANCOVA with nestling age as covariate: $F_{1,11} = 9.70$, $P = 0.010$). Unmanipulated pairs provided significantly different diets to cuckoos and rufous bush robins (chi-square test: $\chi^2_9 = 17.23$, $P = 0.045$; Table 1).

Although nonparasitized broods received on average more parental effort (total amount of food carried/h) than parasitized ones, these differences were not statistically significant (nonparasitized nests: 27.59 ± 14.41 ; parasitized nests: 13.82 ± 4.57 ; one-way ANCOVA with nestling age as covariate: $F_{1,11} = 3.05$, $P = 0.108$).

Feeding in Experimental Conditions

We found no significant differences between the first and second recording sessions (see [Methods](#)) for any variable related to parental effort of experimental pairs (repeated measures ANOVA with nest parasitism status as between-groups factor and age differences as covariate: all NS). However, adults preferred to feed chicks of both species in their original nests (Table 2), although this preference differed between species (interactions between chick species and original or additional nest factors, see Table 2). The percentage of feedings to rufous bush robin chicks when some of them were begging was higher when they were in the original nest than when they were in the additional nest (Table 2), but this was not the case for cuckoo chicks (Table 2). However, since we used values for both sessions, and compared cuckoo and host chick variables from the same experimental nest, the effect of the kind of nest (i.e. original or additional nest) is partially controlled for in the rest of the analyses.

Host experimental broods received almost twice as many prey/h as the experimental cuckoo chicks (Table 3). There were no significant differences in prey sizes (Table 3) or diet received by experimental cuckoo chicks and host experimental broods (chi-square test: $\chi^2_9 = 4.50$, $P = 0.876$; Table 1). Cuckoo chicks received on average half the total amount of food received by host experimental broods (Table 3). In addition, on average, a single experimental host chick received an average amount of food very similar to that received by the experimental cuckoo chick (Table 3). These results were not influenced by whether the experimental pairs were or were not parasitized before the experiment, nor by the differences in age between cuckoo and host chicks fed by the same experimental pair (interactions in Table 3).

Which Chick is Selected to be Fed?

Both species responded to adult feeding in the experimental nests by begging for food at a similar rate (percentage of total feedings to which cuckoo chicks responded by begging: 74.29%; host chicks: 71.43%). However, the cuckoo chick was preferentially fed by adults only when no host chick was begging for food (percentage of feedings to cuckoo chick when no host chick was begging: $63.81 \pm 38.15\%$; when at least one host chick was begging: $22.55 \pm 29.43\%$; repeated measures ANOVA: $F_{1,8} = 8.77$, $P = 0.018$; all interactions NS). On the other hand, the percentage of prey obtained by host broods did not depend on whether the cuckoo chick was begging or not (percentage of feedings obtained by host chicks when cuckoo chick was not begging: $45.24 \pm 38.36\%$; when cuckoo chick was begging: $50.22 \pm 38.67\%$; repeated measures ANOVA: $F_{1,8} = 0.03$, $P = 0.860$; all interactions NS).

Natural versus Experimental Conditions

There were differences in the amount of food carried by the pairs in each treatment (Fig. 2); unmanipulated nonparasitized pairs delivered more food than both unmanipulated parasitized pairs and experimental pairs (least significant difference, LSD, post hoc comparisons in Fig. 2). The average amount of food received by a single rufous bush robin chick did not differ in unmanipulated (8.36 ± 3.29 , $N = 10$) or experimental nests (6.01 ± 1.90 , $N = 11$; LSD post hoc comparison: $P = 0.110$). However, cuckoo chicks received more food in naturally parasitized nests (13.82 ± 4.57 , $N = 4$) than in experimental nests (6.68 ± 5.21 , $N = 11$; LSD post hoc comparison: $P = 0.001$). Thus, the interaction between species and nest treatment (i.e. experimental or unmanipulated) was statistically significant (Fig. 3).

DISCUSSION

Most studies on common cuckoo chick feeding behaviour by adult hosts have been carried out on a single host species, the reed warbler (for other hosts see e.g. [Wyllie](#)

Table 2. Comparisons of variables related to parental effort of experimental pairs with their original nests or additional nests, and the relative success of cuckoo chicks and host broods in both type of nests

Variables	Original nest versus additional nest			Cuckoo chicks			Host broods					
	Type nest effect	Chick species interaction		Original nest	Additional nest	LSD test*	Original nest	Additional nest	LSD test*			
	$F_{1,8}$	P	$F_{1,8}$	P		Mean square	P	Mean square	P			
Prey carried/h	13.48	0.006	7.87	0.023	5.86 ± 5.69	1.36 ± 1.30	2.98	< 0.001	9.99 ± 3.11	3.21 ± 2.78	2.98	< 0.001
Prey size	< 0.01	0.998	0.05	0.824	1.71 ± 0.69	1.67 ± 0.99	0.60	0.898	1.86 ± 0.23	1.89 ± 0.73	0.60	0.927
Amount of food carried/h	12.57	0.008	12.81	0.007	10.59 ± 9.88	2.7 ± 2.47	7.90	< 0.001	18.88 ± 6.23	6.95 ± 5.13	7.90	< 0.001
Percentage of feeds to which chicks begged	3.74	0.089	0.04	0.853	76.84 ± 31.31	56.31 ± 32.29	501.96	0.064	90.03 ± 8.88	66.46 ± 20.96	501.96	0.039

Values are means ± SD.

*Least significant difference test, $df = 8$.

1981; Khayutin et al. 1982; Alvarez 1994b; Kleven et al. 1999; Butchart et al. 2003). Reed warbler adults feed cuckoo chicks and a whole brood of their own chicks with a similar diet and at a similar rate (Brooke & Davies 1989; Grim & Honza 1997). Hence, apparently, cuckoo chicks are able to trick host parents when they are alone in the nest to carry enough food to feed an unusually large chick with an extended nestling period.

Alvarez (1994b) found that rates of weight increase of common cuckoo chicks and broods of rufous bush robin were not significantly different, but, in his figure, growth rates of cuckoo chicks were between those of a whole brood and of a single rufous bush robin chick. We found that parental effort (amount of food delivered) was more than double in nonparasitized than in parasitized nests, but statistical differences did not reach significance. However, the statistical power of this analysis is low (0.34) and nonsignificant results could be caused by the small sample size (sample size necessary to reach a significant result with the detected effect size = 17 per species). In natural parasitized nests, the cuckoo chick received larger prey on average, but fewer than half of the feeds received by whole host broods in nonparasitized nests. So it is possible that the larger prey compensated for the lower feeding rate. The fewer feeds, together with the differences in diet (i.e. prey size) of cuckoo and host chicks (see Results), could be explained by adults being more selective when capturing and/or carrying prey to parasitic chicks. In accordance with that interpretation, we found that for unmanipulated pairs, nonparasitized parents brought a greater variety of prey to the nest than did parasitized ones (Table 1). However, this result could be a by-product of parasitized nests receiving fewer feeds than nonparasitized nests. Although these results contradict those found by Brooke & Davies (1989) and Grim & Honza (1997) in reed warblers (see above), they could be reconciled if rufous bush robins and reed warblers forage differently, the latter being more opportunist than the former (Cramp 1988, 1992). Therefore, these two species may respond in different ways to the same problem (to feed a single, large and hungry chick): increasing prey size (rufous bush robin) or increasing feeding rate (reed warbler).

Why are Experimental Cuckoos not Successful?

When both cuckoo and host chicks were present, the two species received a similar diet and prey size, but the provisioning rate to parasitic chicks was lower than to all host chicks considered together (see Results). As we had predicted, cuckoo chicks in experimental nests received less food than those in naturally parasitized nests. This is unlikely to have been because the parents could not meet the extra demands of mixed broods. Cuckoo, but not host, chicks were negatively affected by being in a mixed-species brood (Fig. 3, interaction factor). Furthermore, in contrast to reed warbler hosts (see e.g. Davies et al. 1998; Kilner et al. 1999), those pairs feeding mixed broods did not work harder than the nonmanipulated pairs; surprisingly, the experimental pairs carried a similar amount of

Table 3. Comparisons of the variables related to parental effort between cuckoo chicks and host broods fed by the experimental pairs

Variables	Host broods	Cuckoo chicks	Chick species effect		Parasitism status interactions		Age difference interactions	
			$F_{1,8}$	P	$F_{1,8}$	P	$F_{1,8}$	P
Prey carried/h	6.60 ± 1.77	3.61 ± 3.21	12.79	0.007	1.37	0.276	1.86	0.209
Average of prey carried per h and per chick	3.19 ± 0.93	3.61 ± 3.21	0.17	0.695	0.74	0.414	2.34	0.165
Prey size	1.88 ± 0.21	2.00 ± 0.375	0.11	0.753	4.93	0.057	4.3	0.072
Amount of food carried/h	12.42 ± 3.65	6.68 ± 5.21	16.46	0.004	1.70	0.229	2.62	0.144
Average of amount of food carried per h and per chick	6.01 ± 1.90	6.68 ± 5.21	0.33	0.581	1.11	0.323	2.91	0.126

Values are means ± SD.

food to unmanipulated parasitized pairs, and less than that carried by unmanipulated nonparasitized pairs (Fig. 2).

In experimental nests, we found that when some of the rufous bush robin chicks were begging, they were selected to be fed by parents independently of whether the cuckoo chick was begging or not. In addition, experimental cuckoo chicks were fed more frequently than their foster siblings only when the rufous bush robin chicks did not beg. Finally, we found no differences on average in feeding rates to single host chicks and cuckoo chicks. Therefore, cuckoo begging behaviour is not enough to elicit rufous bush robin foster parents to feed the cuckoo chick preferentially in an experimental competitive scenario with foster siblings. That conclusion is not affected by a possible bias in feeding preference of host parents, as occurs in other systems (Soler et al. 1995), because naturally parasitized pairs did not feed cuckoo chicks preferentially during the experiments.

Our experimental results agree with those obtained by Davies & Brooke (1988), who found that reed warbler pairs did not feed cuckoo chicks preferentially when they were also feeding one or two reed warbler chicks (but see Grim & Honza 2001 for problems related to the experimental design). Furthermore, in nests of redstarts, *Phoenicurus phoenicurus*, a cavity-nesting bird species, 46% of cuckoo chicks failed to evict nestmates, and most of these cuckoos (56%) died (presumably by starvation), whereas at least

one redstart chick from every mixed brood left the nest (Rutilla et al. 2002). All these results can be explained by a lower ability of parasitic chicks to compete with host chicks, but also by parental discrimination of parasitic chicks, which can occur even in nonevictor brood-parasitic species (Lichtenstein 2001). However, even in the case of parasitic chick recognition, all these results suggest an inability of cuckoo chicks to outcompete foster siblings.

The inability of cuckoos to elicit foster parents to feed them preferentially may have preceded or followed the evolution of eviction behaviour. In the former case the eviction behaviour would be the consequence of that inability, and in the latter the inability to compete with experimental siblings would be the consequence of the eviction behaviour. Although it is difficult to distinguish between these two possibilities with the available information, a discussion of possible scenarios is of interest because it implies different selection pressures favouring the evolution of eviction behaviour.

The first possibility is related to potential hosts distributing food among siblings independently of chick traits (i.e. begging intensity, size, etc.). This seems to be the case for those species possessing a synchronously hatching brood

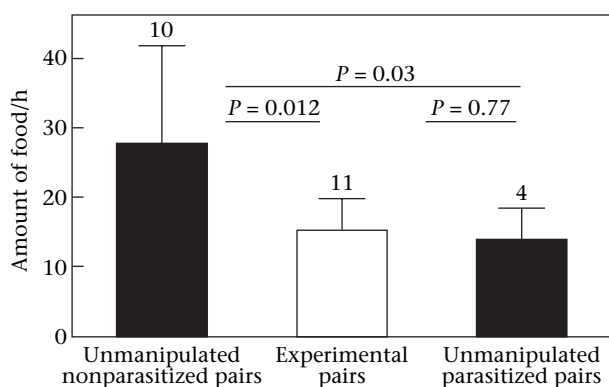


Figure 2. Amount of food carried by rufous bush robin adults in each treatment + SD. One-way ANCOVA with chick age as covariate: $F_{2,21} = 3.9$, $P = 0.036$. Least significant difference post hoc comparisons between groups are shown. Sample sizes are shown above the bars.

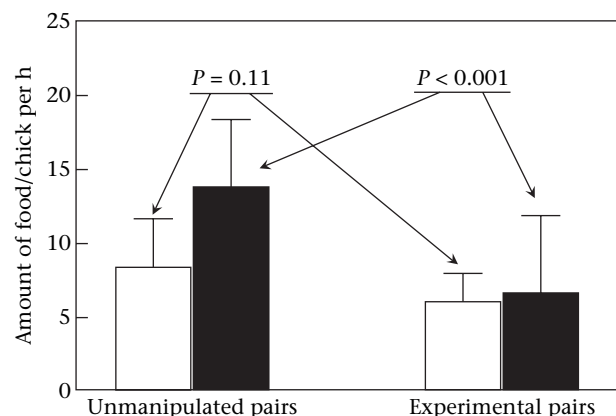


Figure 3. Mean + SD amount of food received/chick per h in the unmanipulated ($N = 14$) and experimental ($N = 11$) nests. Two-way ANCOVA with control or experimental pairs and species as between-groups factors and chick age as covariate. Interaction factor: $F_{1,31} = 4.74$, $P = 0.037$. Least-significant difference post hoc comparisons between unmanipulated and experimental nests for each chick species are also shown. □: Host chick; ■: cuckoo chick.

and where typically all chicks fledge (i.e. clutch size adjuster species, Soler 2001). In nests of such species, a parasitic chick sharing the nest with foster siblings should receive an amount of food similar to that received by a single host chick (Soler 2002). Therefore, because a nonevictor cuckoo chick would not be able to ensure enough food for its development when parasitizing these species, it is possible that the evolution of eviction behaviour in cuckoos can be explained mainly by the specific rules followed by adult hosts among their offspring. In agreement with this possibility, the common cuckoo parasitizes adjuster host species that are smaller than itself and a cuckoo chick needs more food than a single host chick; thus, the only possibility for the cuckoo chick to monopolize parental care and receive enough food is the evolution of eviction behaviour (Soler 2002). However, in disagreement with this possibility, the nonevictor brood-parasitic cowbirds also commonly exploit smaller host species (see e.g. Davies 2000) and the parasitic chick also needs more food than a single host young. There is no evidence that the hosts of cowbirds and common cuckoos differ in the degree of hatching asynchrony.

The second possibility, that the inability of cuckoos to elicit preferential feeding followed the evolution of eviction behaviour, is related to the possibility that the competitive ability of cuckoos was lost after the evolution of eviction behaviour because of the costs associated with some of the begging signals. Some components of begging signals (e.g. call rate) are involved in stimulating food delivery rate to the nest, whereas others (e.g. postures) are concerned with sibling competition and food allocation (see e.g. Kacelnik et al. 1995; Johnstone 2004). Evictor cuckoo chicks could have lost begging signals related to sibling competition. In accordance with that scenario, cuckoo chicks are not able to stretch the legs and neck, as chicks of various host species do in order to place the head as close as possible to the feeding parents. However, evictor cuckoo chicks, by exaggerating their call rate, and because they receive all the food brought to the nest, are able to trick the foster parents and obtain enough food for optimal growth (Kilner et al. 1999; Soler & Soler 1999; Grim & Honza 2001; Butchart et al. 2003). Because common cuckoo chicks do not need to compete with foster siblings, they could have lost the other begging signals (i.e. postures), since these could increase the risk of falling from a small nest (Davies et al. 1998) and/or losing them could reduce the cost of producing an exaggerated call rate (Lotem 1998). In agreement with this idea, although our experiment prevented cuckoo and host chicks from competing for positions related to parent arrival, or sibling aggression, they never moved in relation to parent arrivals in natural or experimental nests; they simply opened their gapes and gave begging calls. Thus, although we cannot exclude the possibility that cuckoo chicks compete for a position with experimental foster siblings, this is unlikely.

One way to estimate the probability of occurrence of the two possibilities discussed above is to study eviction behaviour in a phylogenetic context looking at contrasts (i.e. events of appearance and disappearance) of eviction behaviour within a brood-parasitic clade. However, whether using phylogenies inferred from either osteological (Hughes 2000) or molecular data (Aragón et al. 1999;

Sorenson & Payne 2002), the number of contrasts detected is very low. Although eviction behaviour is unknown for some species of cuckoos (for instance, lesser cuckoo, *Cuculus poliocephalus*; see also Payne 1997; or appendix in Krüger & Davies 2002), contrasts appear only within the common koel, *Eudynamis scolopacea*, clade, for which some Indian subspecies do not evict host siblings. None the less, it is clear that, before brood parasitism appeared within a clade, the ancestral cuckoos shared the nest with siblings and therefore competed with them to be fed by parents, although we do not know whether that ancestral competitive ability was effective after brood parasitism evolved. It is possible that, depending on the rules followed by host parents for distributing food among chicks, eviction behaviour appeared only in clades parasitizing hosts that distribute food evenly among offspring, whereas for other brood-parasitic clades parasitizing hosts with high sibling competition, brood-parasitic chicks had an advantage because of some specific traits (larger size, short incubation period, etc.; Soler 2002). Although natural selection would favour the loss of competitive ability in the first case because of the associated costs, in the second case natural selection would favour the exaggeration of some begging component related to sibling competition. Then, only by detecting begging signals related to sibling competition in nonbrood-parasitic cuckoos and studying those target signals in brood-parasitic cuckoos with and without ejection behaviour, would it be possible to know whether or not the inability of some cuckoos to elicit preferential feeding preceded the evolution of ejection behaviour.

In conclusion, our results suggest that the costly eviction behaviour of cuckoos is of selective advantage because it prevents competition with foster siblings for parental care where its exaggerated begging behaviour is not enough to obtain the food needed for development. These results could be explained by (1) cuckoo chicks lacking begging signals related to sibling competition, (2) host adults tending to distribute food evenly among the brood, and/or (3) host adults recognizing a cuckoo chick when their own chicks are present.

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