#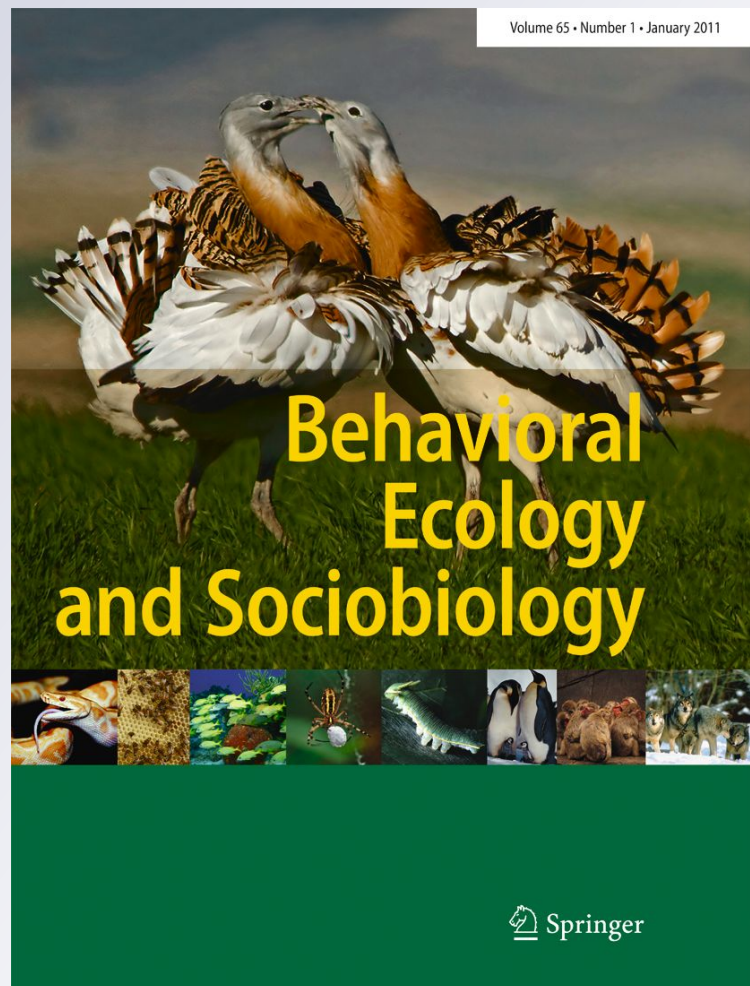 Brood parasitism disproportionately increases nest provisioning and helper recruitment in a cooperatively breeding bird

Cynthia A. Ursino, María C. De Mársico, Mariela Sued, Andrés Farall & Juan C. Reboreda

Springer

Springer

ORIGINAL PAPER

Brood parasitism disproportionately increases nest provisioning and helper recruitment in a cooperatively breeding bird

**Cynthia A. Ursino · María C. De Mársico ·
Mariela Sued · Andrés Farall · Juan C. Reboreda**

Abstract Obligate avian brood parasites lay their eggs in nests of other species (hosts), which raise parasitic young. Parasitic nestlings are likely to influence host's parental behaviours as they typically beg for food more vigorously than young host for a given hunger level. However, few studies have tested this idea, with conflicting results. These prior studies were largely limited to biparental hosts, but little is known about the effect of brood parasitism on parental behaviours in hosts that breed cooperatively. We followed a multimodel approach to examine the effect of brood parasitism on nest provisioning and helper recruitment in the baywing (*Agelaioides badius*), a cooperative breeder parasitised by screaming (*Molothrus rufoaxillaris*) and shiny (*Molothrus bonariensis*) cowbirds. Multimodel inference results indicated that feeding visits increased with nestling age, cooperative group size and number of cowbird nestlings in the brood. Brood size had little influence on feeding visits, which further suggests that baywings adjusted their provisioning effort in response to cowbird parasitism. In addition, nests parasitised artificially with shiny cowbird eggs or hatchlings recruited more helpers than unmanipulated nests having only host or screaming cowbird young. Our results provide novel evidence that brood parasitism and cooperative breeding interact in determining the levels of nest provisioning.

Keywords *Agelaioides badius* · Brood parasitism · Cooperative breeding · *Molothrus* · Nest provisioning

Introduction

Obligate avian brood parasites lay their eggs in nests of individuals of other species (hosts) that raise the parasitic offspring at the expense of their own reproductive success (Rothstein 1990). The young of some brood parasites (e.g. the common cuckoo, *Cuculus canorus*) causes the failure of host brood by eliminating all host eggs and nestlings from the nest soon after hatching (Davies 2000). In other species like cowbirds (*Molothrus* spp.), parasitic nestlings do not attack young host directly but may cause the loss of all or some host nestlings by outcompeting them for food (Lorenzana and Sealy 1999). Typically, parasitic nestlings exhibit more exaggerated begging displays than the young host for a given hunger level and such intense begging may influence host parental behaviour (Davies et al. 1998; Dearborn 1998; Lichtenstein and Sealy 1998; Lichtenstein and Dearborn 2004). However, relatively few studies have examined the influence of parasitic young on nest provisioning by host parents, with varying results. For instance, previous studies indicated that some hosts of the brown-headed cowbird (*Molothrus ater*) provisioned parasitised nests at higher rates than unparasitised ones (Dearborn et al. 1998; Hauber and Montenegro 2002; Hoover and Reetz

C. A. Ursino · M. C. De Mársico (✉) · J. C. Reboreda
Departamento de Ecología, Genética y Evolución, Facultad
de Ciencias Exactas y Naturales, Universidad de Buenos Aires,
Pabellón II Ciudad Universitaria,
C1428EGA Buenos Aires, Argentina
e-mail: de_marsico@ege.fcen.uba.ar

M. Sued
Instituto del Cálculo, Facultad de Ciencias Exactas y Naturales,
Universidad de Buenos Aires,
Buenos Aires, Argentina

A. Farall
Departamento de Ciencias de la Atmósfera y los Océanos,
Facultad de Ciencias Exactas y Naturales,
Universidad de Buenos Aires,
Buenos Aires, Argentina

2006), but others failed to find a clear effect of parasitism on host-provisioning rates (Glassey and Forbes 2003; Rivers et al. 2010). Moreover, these prior studies were largely limited to host species with biparental or uniparental care, whereas little is known about the effect of brood parasitism on parental behaviours in hosts with cooperative breeding.

In cooperatively breeding species, parents are assisted by a number of helpers at the nest that contribute to offspring care. In some species, helpers may respond to changes in brood demand by increasing their contribution to nest provisioning with begging intensity or nestling age (Wright 1998; MacGregor and Cockburn 2002; McDonald et al. 2009). In turn, helpers' contribution may influence the levels of investment in brood care by parents, which may reduce their provisioning rate as the contribution of other group members increases (Hatchwell 1999; Wright and Dingemanse 1999; Heinsohn 2004; Canestrari et al. 2007). Such flexible provisioning rules might be particularly beneficial for host parents, if helping ameliorates the costs of raising parasitised broods. However, although many host species breed cooperatively, interactions between brood parasitism and cooperative breeding have been barely explored so far (Poiani and Elgar 1994; Langmore and Kilner 2007; Canestrari et al. 2009). Hence, whether brood parasitism can influence parental behaviours and social dynamics in cooperative hosts remains poorly understood.

In this study, we examined the effect of brood parasitism on nest provisioning and helper recruitment in a cooperative breeder, the baywing (*Agelaioides badius*). This species is the primary host of the screaming cowbird (*Molothrus rufoaxillaris*) and a secondary host of the shiny cowbird (*Molothrus bonariensis*; Ortega 1998). Baywings are socially monogamous and single brooded (Fraga 1991). Assisted pairs typically have one to three helpers, which are mostly sons and join the breeding pair after hatching (Fraga 1991). Helpers contribute to mob predators and provision the nest and increase in number with nestling age, suggesting that additional individuals can be recruited as brood requirements increase (Fraga 1991). Flexible helper recruitment may play a major role in increasing overall nest-provisioning rates and thus enhancing nestling survival when parental provisioning alone is insufficient to fulfil brood demand (Reyer 1980). On the other hand, the presence of helpers may contribute to make the nest more susceptible to interspecific brood parasitism if increased parental activity makes the nest more conspicuous to parasitic females or if parasitic females preferentially parasitise nests attended by larger groups, which are more likely to rear successfully the parasitic young (Poiani and Elgar 1994). Nevertheless, a few available studies that aimed to test these hypotheses found little evidence favouring a positive relationship between cooperative breeding and brood parasitism rates (Poiani and Elgar 1994; Langmore and Kilner 2007; Canestrari et al. 2009).

Our primary aim was to examine the influence of cowbird nestlings on nest-provisioning rates. Screaming and shiny cowbird nestlings are slightly larger than young baywing, grow at faster rates and beg more intensively than young host at similar hunger levels (Lichtenstein 2001; Lichtenstein and Dearborn 2004; De Mársico et al. 2010), thus it is likely that broods with parasitic nestlings demand disproportionately more food than those with host offspring alone and hosts respond to such demand by increasing the nest-provisioning rates. Alternatively, cowbird nestlings may have little influence on host parental effort but baywings may adjust overall nest-provisioning rates in response to other factors such as total brood size, nestling age or cooperative group size (Fraga 1991). We used a multimodel approach to identify which of these alternatives better explain overall nest-provisioning rates in baywings. Additionally, we analysed the relationship between the presence of cowbird nestlings in the brood and cooperative group size in order to test whether baywings recruit additional helpers in response to parasitism.

Materials and methods

Study area and data collection

The study was conducted at "Reserva El Destino" (35°08′ S, 57°23′ W) in the province of Buenos Aires, Argentina. The study site is a flat area of 320 ha within the Biosphere Reserve "Parque Costero del Sur" (MAB-UNESCO). The area comprises a mosaic of marshy grasslands and woodland patches dominated by *Celtis tala* and *Scutia buxifolia*. Baywings are year-round residents in the area and breed from early December to late February. We conducted this study during the breeding seasons of 2006–2007, 2007–2008 and 2009–2010. Baywings rarely built their own nest but breed in old nests of other species (e.g. *Phacellodomus* spp., *Synallaxis* spp. and *Furnarius rufus*), secondary cavities and nest boxes (Fraga 1988). Near 25% of baywing nests found during this study occurred in wooden nest boxes located in the study area since 2003. The boxes were $30 \times 20 \times 16$ cm (height, width and depth) and had a circular entrance hole of 5.8 cm of diameter and an opening roof to allow nest inspection. They were attached to trees at a height of 1.8–2.5 m on the edges of woodland patches and separated from each other by at least 50 m. Annual parasitism rates in baywing nests during the study ranged from 94% to 100% for screaming cowbirds (2006–2007, 94%, $n=70$ nests; 2007–2008, 100%, $n=23$; 2009–2010, 100%, $n=54$) and 0% to 11% for shiny cowbirds (2006–2007, 7%, $n=70$ nests; 2007–2008, 0%, $n=23$; 2009–2010, 11%, $n=54$).

From all nests found ($n=147$), we monitored 128 baywing nests where hosts lay eggs (5 unparasitised, 113 parasitised by screaming cowbirds only and 10 parasitised by screaming and shiny cowbirds). Given the low frequency of shiny cowbird parasitism in baywing nests, we artificially parasitised a subsample of 25 nests by adding a single shiny cowbird egg ($n=21$) or hatchling ($n=4$) collected from nearby, multiple parasitised nests of chalk-browed mockingbird (*Mimus saturninus*). Sample size for data analysis was 45 nests that survived to the nestling stage of which 12 were unparasitised, 27 were parasitised by screaming cowbirds and 6 were parasitised by screaming and shiny cowbirds. All the latter were artificially parasitised with shiny cowbird eggs or hatchlings prior to data collection. We checked nests every 1 to 3 days until they fledged chicks or failed. In each visit, we recorded nest content and cooperative group size, defined as the number of adult baywings present simultaneously in the vicinity of the nest that mobbed us or gave alarm calls during nest checking. Every egg and nestling was marked with waterproof ink and assigned to baywing, screaming or shiny cowbird using egg shell spotting or skin and bill coloration as diagnostic cues (Fraga 1979; De Mársico et al. 2010). For each nest, we determined the laying date of the first host egg (i.e. clutch initiation date) either directly or through backdating from hatching dates.

We video recorded the feeding visits by adult baywings at 23 nests using an analogue Sony Hi8 CCD camcorder placed on a tripod at less than 5 m from the nest. Pilot-recording sessions showed that video cameras placed near the nests did not affect baywings' parental behaviour. Video recordings lasted 4 h and were done during the morning (7:00 a.m.–12:00 p.m.) when nestlings were 3–4, 6–7 and 9–10 days of age. Simultaneously to recording sessions, we conducted focal observations of the nest to further determine cooperative group size. Observations lasted at least 1 h and were done using 7×50 binoculars from a blind located about 15–20 m far from the nest. We calculated the frequency of feeding visits by cooperative groups from videotapes as the number of times an adult baywing (parent or helper) entered the nest carrying food in its bill.

Data analysis

We analysed the effect of brood parasitism on the number of feeding visits by cooperative groups using generalized linear mixed models (GLMM) with log link function and Poisson error structure. Models were fitted by Laplace approximation using lmer function of package lme4 in R 2.11.0 (R Development Core Team 2008). Explanatory variables were cooperative group size (i.e. the number of provisioning adults), nestling age (categorized as 3–4, 6–7 and 9–10 days), host brood size (i.e. the number of baywing nestlings) and the number of cowbird nestlings in the brood (screaming plus shiny cowbirds). Models included nest identity as a random effect and recording span as a variable offset because some recording sessions were interrupted by inclement weather. All possible models were evaluated and parameter values were estimated using information theoretic procedures (Burnham and Anderson 1998; Symonds and Moussalli 2011). The procedures allow model uncertainty to be included in both model evaluation and derivation of parameter estimates. So, inferences were not based on a single model and relative strengths of parameter estimates derived from all models were used. This resulted in 16 candidate models according to all possible combinations between the four explanatory variables. For each candidate model, we computed the Akaike information criterion corrected by small sample size (AIC_c). We ranked these 16 candidate models by the AIC_c criterion and computed the differences (Δi) between the AIC_c of the candidate models and the AIC_c of the best model (lowest AIC_c) as well as the Akaike weights for each model (Table 1). We calculated average parameter estimates and their standard deviations estimates following Burnham and Anderson (1998). These are presented in Table 2 (see Symonds and Moussalli 2011 for further details). In addition, parameter likelihoods (sum of weights across all models including the parameter) were computed. The best ranked model was considered to evaluate its goodness of fit in comparison with the null model. We conducted a likelihood ratio test and a goodness of fit F test against the null model, which includes just an intercept and a variance parameter for the random effect (i.e. nest identity). In addition, because both likelihood ratio test and F test rely on distributional assumptions over the test statistics, we performed a Monte Carlo simulation under the null model. The intercept and variance parameter values used for the data-generating process were those estimated under the null model.

To analyse the effect of cowbird parasitism on helper recruitment, we used a subset of 35 nests that survived until fledging. We tested the relationship between cooperative group size at days 9–10 and parasitism status using a Kruskal–Wallis test. In addition, we used Spearman rank correlations to test the relationship between helper recruitment and date of the breeding season and brood size, which may confound the effect of brood parasitism. Specifically, we tested a positive correlation between: (1) group size and clutch initiation date, as predicted if baywings recruited additional helpers among former breeders that failed in their own breeding attempt (Hatchwell et al. 2004) and (2) group size and brood size, as predicted if baywings recruit additional helpers just in response to the number of nestlings in the nest. Statistical tests were done with StatView 5.0 (SAS Institute 1998). Tests were two tailed and significance was accepted at $P<0.05$.

Table 1 Models were ranked according to the Akaike information criterion corrected for small sample size (AIC$_c$). The null model included only the intercept and nest identity as a random factor

	Candidate models	K	AIC$_c$	Δ_i	w_i	acc w_i	ER
1	Int+age(2)+age(3)+BP+GS	6	183.50	0.00	0.550	0.550	1.000
2	Int+age(2)+age(3)+GS	5	185.32	1.82	0.221	0.771	0.402
3	Int+age(2)+age(3)+BW+BP+GS	7	186.20	2.70	0.143	0.914	0.260
4	Int+age(2)+age(3)+BW+GS	6	187.46	3.96	0.076	0.990	0.138
5	Int+age(2)+age(3)+BP	5	192.29	8.79	0.007	0.997	0.013
6	Int+age(2)+age(3)+BW+BP	6	194.86	11.36	0.002	0.999	0.004
7	Int+age(2)+age(3)	4	195.70	12.20	0.001	1.000	0.002
8	Int+age(2)+age(3)+BW	5	197.99	14.49	0.000	1.000	0.000
9	Int+BP+GS	4	207.60	24.10	0.000	1.000	0.000
10	Int+GS	3	207.76	24.26	0.000	1.000	0.000
11	Int+BW+GS	4	209.53	26.03	0.000	1.000	0.000
12	Int+BW+BP+GS	5	209.88	26.38	0.000	1.000	0.000
13	Int+BP	3	235.12	51.62	0.000	1.000	0.000
14	Int	2	235.98	52.48	0.000	1.000	0.000
15	Int+BP+GS	4	237.50	54.00	0.000	1.000	0.000
16	Int+BW	3	238.02	54.52	0.000	1.000	0.000

Age, nestling age categorized as 3–4, 6–7 (*age* 2), and 9–10 (*age* 3) (days of age), *BP* number of parasitic nestlings in the brood, *GS* cooperative group size, *BW* number of host nestlings in the brood, *K* number of explanatory parameters in the model; $\Delta_i = \text{AIC}_{c(i)} - \text{AIC}_{c(min)}$; w_i, Akaike weight; acc w_i, cumulative Akaike weight; *ER* evidence ratio

Results

The results of multimodel inference supported an effect of helpers at the nest, nestling age and cowbird parasitism on the number of feeding visits (Table 1). These variables were better supported than the number of baywing nestlings in explaining the rate of feeding visits (Table 2). These conclusions were based on multimodel confidence intervals and likelihood parameter values (Table 2). The best ranked model included group size, nestling age and the number of parasitic nestlings in the brood as predictors (Table 1). The likelihood ratio test and the goodness of fit *F* test against the null model were both statistically significant at $P < 0.001$, and the Monte Carlo simulation under the null model was significant at $P < 0.0001$.

Helpers occurred at 40% of 35 nests that survived until fledging (10 unparasitised, 21 parasitised by screaming cowbird only and 4 parasitised by screaming and shiny cowbirds; Table 3). Cooperative group size (range, 2–5) did not correlate with clutch initiation date (Spearman rank correlation, $r = 0.11$, $P = 0.52$) but correlated positively with total brood size ($r = 0.36$, $P = 0.034$). Nevertheless, this correlation was not significant when nests parasitised by both screaming and shiny cowbirds were excluded from the analysis ($r = 0.27$, $P = 0.093$, $n = 31$ nests). Nests with mixed parasitism ($n = 4$) recruited more helpers than unparasitised nests ($n = 10$) and nests parasitised by screaming cowbird

only ($n = 21$; Kruskal–Wallis test, 8.49, $P = 0.014$, post hoc comparisons $P < 0.05$; Fig. 1).

Discussion

Our results strongly suggest that baywings followed flexible provisioning rules and adjusted levels of nest provisioning in response to changes in brood demand related to nestling age and brood parasitism. Also, parameter estimates showed that host brood size had a lower weight than the number of cowbird nestlings as explanatory variables, suggesting that cowbird nestlings were more likely to influence the frequency of feeding visits than the host's own young. This finding is consistent with previous observations for other hosts of the brown-headed cowbird showing a higher rate of nest visits at parasitised broods compared to unparasitised ones (*Passerina cyanea*, Dearborn et al. 1998; *Sayornis phoebe*, Hauber and Montenegro 2002; *Protonotaria citrea*, Hoover and Reetz 2006; *Agelaius phoenicius*, S. Forbes, personal communication) and provides novel evidence that cooperative breeders may follow similar provisioning rules than biparental or uniparental hosts when faced to cowbird parasitism.

Parasitic nestlings can stimulate hosts to increase nest-provisioning levels beyond those observed at unparasitised

Table 2 Parameter estimates and standard erros for all models are considered. Predictors are: intercept, age, nestling age categorized as 3-4, 6-7 (age2) and 9-10 (age3) (days of age). Average parameter estimates with their standard errors and parameter likelihood are shown in the last lines. See Symonds and Moussalli (2011) for further details

	Int	Age (2)	Age (3)	BW	BP	GS
1	−2.206 (0.159)	0.215 (0.056)	0.332 (0.063)		0.136 (0.064)	0.175 (0.052)
2	−2.052 (0.140)	0.216 (0.056)	0.315 (0.062)			0.184 (0.051)
3	−2.166 (0.254)	0.216 (0.056)	0.331 (0.063)	−0.012 (0.057)	0.133 (0.066)	0.177 (0.052)
4	−1.934 (0.221)	0.218 (0.056)	0.314 (0.062)	−0.038 (0.054)		0.188 (0.051)
5	−1.811 (0.107)	0.236 (0.056)	0.404 (0.059)		0.156 (0.064)	
6	−1.859 (0.233)	0.235 (0.056)	0.404 (0.059)	0.013 (0.055)	0.159 (0.065)	
7	−1.611 (0.070)	0.240 (0.056)	0.390 (0.059)			
8	−1.521 (0.206)	0.242 (0.056)	0.390 (0.059)	−0.027 (0.057)		
9	−2.221 (0.161)				0.105 (0.065)	0.268 (0.049)
10	−2.084 (0.137)					0.267 (0.048)
11	−1.946 (0.226)			−0.044 (0.055)		0.271 (0.049)
12	−2.129 (0.264)			−0.027 (0.058)	0.1 (0.068)	0.271 (0.049)
13	−1.549 (0.102)				0.120 (0.066)	
14	−1.398 (0.063)					
15	−1.562 (0.238)			0.003 (0.057)	0.121 (0.068)	
16	−1.295 (0.213)			−0.030 (0.059)		
$\hat{\hat{\beta}}$	−2.144	0.22	0.325	−0.020	0.138	0.181
se	0.195	0.06	0.061	0.013	0.044	0.050
$\tilde{\beta}$	−2.144	0.22	0.325	−0.004	0.097	0.179
se	0.201	0.06	0.061	0.028	0.063	0.050
w	1	1	1	0.221	0.702	0.99

se standard error, w parameter likelihoods, Int intercept, BP number of parasitic nestlings in the brood, GS cooperative group size, BW number of host nestlings in the brood

broods either directly, by exhibiting exaggerated begging displays that tune into the host's parent–offspring communication system (i.e. supernormal stimulus hypothesis, Davies et al. 1998; Grim and Honza 2001), or indirectly by inducing host nestlings to beg more intensively (Pagnucco et al. 2008). Available evidence indicates that both screaming and shiny cowbird nestlings beg more intensively than the young host after controlling for their hunger level (Lichtenstein 2001; Lichtenstein and Dearborn 2004), but further experimental work is needed to assess how parasitic cowbirds influence host's parental behaviours. A previous study have failed to find a clear effect of brown-headed cowbird parasitism on nest-provisioning

levels in an intermediate-sized host (the red-winged blackbird, A. phoenicius; Rivers et al. 2010), which contrasts markedly with our results. Interestingly, this study found little differences in begging intensity between the cowbird and the red-winged blackbird nestlings, which in turn may explain why host parents did not provide significantly more food to singly parasitised than unparasitised broods (Rivers et al. 2010).

The results of multimodel inference also supported a positive effect of group size on feeding visits, suggesting that breeders did not fully compensate for helpers' contribution to nest provisioning (Hatchwell 1999; Canestrari et al. 2008; Kingma et al. 2010). However, even a partial reduction in the

Table 3 Brood composition of baywing nests that survived until fledging

Parasitism status	n	Host	Screaming cowbird	Shiny cowbird	Total
Unparasitised	10	3.6±0.3 (2–5)			3.6±0.3 (2–5)
Screaming cowbird only	21	2.4±0.1 (0–4)	1.5±0.2 (1–4)		4.1±0.3 (1–7)
Screaming and shiny cowbird	4	3.8±0.3 (3–4)	1.3±0.3 (1–2)	1.0±0.0	6.0±0.0

Values are mean±s.e. number of nestlings of each species and total brood size by days 9–10 of the nestling stage. Ranges are given in parentheses
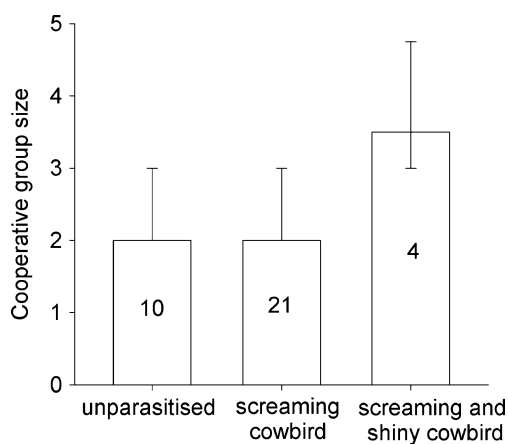
Fig. 1 Group size by days 9–10 of the nestling stage at baywing nests that were unparasitised, parasitised by screaming cowbird only and parasitised by screaming and shiny cowbird. *Bars* indicate median number of adult baywings per nest (parents plus helpers) and interquartile ranges. Sample sizes are given within *bars*

levels of parental investment in response to helpers' assistance may allow breeders to enhance their prospects for survival and future reproductive success (Hatchwell 1999; Kingma et al. 2010). Furthermore, the contribution of helpers to parental care may allow host parents to reduce the detrimental effects of parasitism on their reproductive success, with potential consequences for host–parasite coevolution. For example, larger groups might be able to provide more food to the nest at one time or to synchronize their feeding visits more often, which in turn may limit the strength of competition between host and parasitic nestlings and enhances the survival of host nestling at parasitised broods (Heinsohn et al. 1988; Raihani et al. 2010; Shen et al. 2010).

We found that nests parasitised by screaming and shiny cowbirds had more helpers than unparasitised nests and those parasitised solely by screaming cowbirds. Group size showed no clear association with brood size when nests with mixed parasitism where excluded from the analysis, and it did not correlate with clutch initiation date, as it might occur if former breeders secondarily help other breeding pairs after failing in their own breeding attempts (Valencia et al. 2003; Hatchwell et al. 2004). Hence, the observed differences in group size cannot be attributed to either of these factors alone. Furthermore, nests with mixed parasitism were parasitised artificially with shiny cowbird eggs or hatchlings before helpers joined the breeding pair (i.e. blindly to cooperative group size). In consequence, it seems likely that recruitment of additional helpers in cooperative groups occurred in response to brood parasitism. However, we cannot completely dismiss the possibility that brood size and cowbird parasitism interact in determining cooperative group size. For instance, breeding pairs may recruit additional helpers when brood demand increases beyond a certain threshold, which in turn may be more easily achieved at nests with mixed parasitism. More experimental work is needed to determine the cues that trigger helper recruitment at parasitised nests in baywings.

A positive relationship between brood parasitism and the presence of helpers at the nest could also arise if parasitic females preferentially choose nests attended by larger groups to lay their eggs, as it has been previously suggested (e.g. Poiani and Elgar 1994). However, this hypothesis seems unlikely to explain our results, first because helpers were seldom recruited during the egg-laying and incubation stages, when most parasitic events occur (De Mársico and Reboreda 2008) and second because larger group sizes occurred at nests that were artificially parasitised before helpers appeared. Similarly, previous studies in other cooperatively breeding hosts failed to find a positive effect of helpers at the nest on the likelihood of interspecific brood parasitism (Langmore and Kilner 2007; Canestrari et al. 2009).

Flexible helper recruitment was reported previously for baywings, although not in relation to cowbird parasitism (Fraga 1991). This previous report identified nestling age as the most influential factor on nest-provisioning rate and helper recruitment, but it did not consider separately the confounding effect of parasitism. The recruitment of additional helpers associated to the presence of parasitic nestlings in the brood might allow host parents to ameliorate the costs of raising parasitised broods, particularly if parental provisioning alone does not meet brood requirements (Reyer 1980). Interestingly, the observed differences in group size between broods parasitised by screaming cowbird only and those parasitised by screaming and shiny cowbirds point towards a differential effect of cowbird species on brood demand that deserves further investigation.

Altogether, our results indicate that screaming and shiny cowbird nestlings can influence overall nest-provisioning rates and helper recruitment in a cooperatively breeding host. Future studies are needed to disentangle the mechanisms underlying these effects and the consequences of helping to host parental investment and reproductive success.

References

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, New York

Canestrari D, Marcos JM, Baglione V (2007) Costs of chick provisioning in cooperatively breeding crows: an experimental study. Anim Behav 73:347–357. doi:10.1016/j.anbehav.2006.04.013

Canestrari D, Marcos JM, Baglione V (2008) Reproductive success increases with group size in cooperative carrion crows, *Corvus corone corone*. Anim Behav 75:403–416. doi:10.1016/j.anbehav.2007.05.005

Canestrari D, Marcos JM, Baglione V (2009) Cooperative breeding in carrion crows reduces the rate of brood parasitism by great spotted cuckoos. Anim Behav 77:1337–1344. doi:10.1016/j.anbehav.2009.02.009

Davies NB (2000) Cuckoos, cowbirds and other cheats. T & AD Poyser, London

Davies NB, Kilner RM, Noble DG (1998) Nestling cuckoos, *Cuculus canorus*, exploit hosts with begging calls that mimic a brood. Proc R Soc B 265:673–678. doi:10.1098/rspb.1998.0346

De Mársico MC, Reboreda JC (2008) Egg-laying behavior in screaming cowbirds: why does a specialist brood parasite waste so many eggs? Condor 110:143–153

De Mársico MC, Mahler B, Reboreda JC (2010) Reproductive success and nestling growth of the baywing parasitized by screaming and shiny cowbirds. Wilson J Ornithol 122:417–431. doi:10.1676/09-140.1

Dearborn DC (1998) Begging behaviour and food acquisition by brown-headed cowbird nestlings. Behav Ecol Sociobiol 43:259–270. doi:10.1007/s002650050490

Dearborn DC, Anders AD, Thompson FR, Faaborg J (1998) Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor 100:326–334

Fraga RM (1979) Differences between nestlings and fledglings of screaming and bay-winged cowbirds. Wilson Bull 91:151–154

Fraga RM (1988) Nests sites and breeding success of bay-winged cowbirds (*Molothrus badius*). J Ornithol 129:175–183

Fraga RM (1991) The social system of a communal breeder, the bay-winged cowbird *Molothrus badius*. Ethology 89:195–210

Glassey B, Forbes S (2003) Why brown-headed cowbirds do not influence red-winged blackbird parent behaviour. Anim Behav 65:1235–1246. doi:10.1006/anbe.2003.2168

Grim T, Honza M (2001) Does supernormal stimulus influence parental behaviour of the cuckoo's host? Behav Ecol Sociobiol 49:322–329. doi:10.1007/s002650000295

Hatchwell BJ (1999) Investment strategies of breeders in avian cooperative breeding systems. Am Nat 154:205–219

Hatchwell BJ, Russell AF, McColl ADC, Ross DJ, Fowlie MK, McGowan A (2004) Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. Behav Ecol 15:1–10. doi:10.1093/beheco/arg091

Hauber ME, Montenegro K (2002) What are the costs of raising a brood parasite? Comparing host parental care at parasitized and non-parasitized broods. Etología 10:1–9

Heinsohn RG (2004) Parental care, load-lightening and costs. In: Koenig W, Dickinson J (eds) Ecology and evolution of cooperative breeding in birds. Cambridge University Press, Cambridge, pp 67–80

Heinsohn RG, Cockburn A, Cunningham RB (1988) Foraging, delayed maturation, and advantages of cooperative breeding in white-winged choughs, *Corcorax melanorhamphos*. Ethology 77:177–186

Hoover JP, Reetz MJ (2006) Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. Oecologia 149:165–173. doi:10.1007/s00442-006-0424-1

Kingma SA, Hall ML, Arriero E, Peters A (2010) Multiple benefits of cooperative breeding in purple-crowned fairy-wrens: a consequence of fidelity? J Anim Ecol 79:757–768. doi:10.1111/j.1365-2656.2010.01697.x

Langmore NE, Kilner RM (2007) Breeding site and host selection by Horsfield's bronze-cuckoos, *Chalcites basalis*. Anim Behav 74:995–1004. doi:10.1016/j.anbehav.2007.02.028

Lichtenstein G (2001) Selfish begging by screaming cowbird, a mimetic brood parasite of the bay-winged cowbird. Anim Behav 61:1151–1158. doi:10.1006/anbe.2000.1688

Lichtenstein G, Dearborn DC (2004) Begging and short-term need in cowbird nestlings: how different are brood parasites. Behav Ecol Sociobiol 56:352–359

Lichtenstein G, Sealy SG (1998) Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. Proc R Soc B 265:249–254. doi:10.1098/rspb.1998.0289

Lorenzana JC, Sealy SG (1999) A meta-analysis of the impact of parasitism by brown-headed cowbirds on its hosts. Stud Avian Biol 18:241–253

MacGregor NA, Cockburn A (2002) Sex differences in parental response to begging nestlings in superb fairy-wrens. Anim Behav 63:923–932. doi:10.1006/anbe.2001.1991

McDonald PG, Kazem AJN, Wright J (2009) Cooperative provisioning dynamics: fathers and unrelated helpers show similar responses to manipulations of begging. Anim Behav 77:369–376. doi:10.1016/j.anbehav.2008.10.009

Ortega C (1998) Cowbirds and other brood parasites. University of Arizona Press, Tucson

Pagnucco K, Zanette L, Clinchy M, Leonard ML (2008) Sheep in wolf's clothing: host nestling vocalizations resemble their cowbird competitor's. Proc R Soc B 275:1061–1065. doi:10.1098/rspb.2007.1706

Poiani A, Elgar MA (1994) Cooperative breeding in the Australian avifauna and brood parasitism by cuckoos (*Cuculidae*). Anim Behav 47:697–706. doi:10.1006/anbe.1994.1094

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Raihani NJ, Nelson-Flower MJ, Moyes K, Browning LE, Ridley AL (2010) Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. J Anim Ecol 79:44–52. doi:10.1111/j.1365-2656.2009.01606.x

Reyer H-U (1980) Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis rudis* L.). Behav Ecol Sociobiol 6:219–227. doi:10.1007/BF00569203

Rivers JW, Loughin TM, Rothstein SI (2010) Brown-headed cowbird nestlings influence nestmate begging, but not parental feeding, in hosts of three distinct sizes. Anim Behav 79:107–116. doi:10.1016/j.anbehav.2009.10.009

Rothstein SI (1990) A model system for coevolution: avian brood parasitism. Ann Rev Ecol Syst 21:481–508

SAS Institue (1998) StatView user's guide. Version 5.0. SAS Institute, Cary

Shen S-F, Chen H-C, Vehrencamp SL, Yuan H-W (2010) Group provisioning limits sharing conflict among nestlings in joint-nesting Taiwan yuhinas. Biol Lett 6:318–321. doi:10.1098/rsbl.2009.0909

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21. doi:10.1007/s00265-010-1037-6

Valencia J, de la Cruz C, González B (2003) Flexible helping behaviour in the azure-winged magpie. Ethology 109:545–558. doi:10.1046/j.1439-0310.2003.00896.x

Wright J (1998) Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behav Ecol Sociobiol 42:423–429. doi:10.1007/s002650050456

Wright J, Dingemanse NJ (1999) Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. Anim Behav 58:345–350. doi:10.1006/anbe.1999.1152