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Differential reproductive success favours strong host preference in a highly specialized brood parasite

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Obligate avian brood parasites show dramatic variation in the degree to which they are host specialists or host generalists. The screaming cowbird *Molothrus rufoaxillaris* is one of the most specialized brood parasites, using a single host, the bay-winged cowbird (*Agelaioides badius*) over most of its range. Coevolutionary theory predicts increasing host specificity the longer the parasite interacts with a particular avian community, as hosts evolve defences that the parasite cannot counteract. According to this view, host specificity can be maintained if screaming cowbirds avoid parasitizing potentially suitable hosts that have developed effective defences against parasitic females or eggs. Specialization may also be favoured, even in the absence of host defences, if the parasite's reproductive success in alternative hosts is lower than that in the main host. We experimentally tested these hypotheses using as alternative hosts two suitable but unparasitized species: house wrens (*Troglodytes aedon*) and chalk-browed mockingbirds (*Mimus saturninus*). We assessed host defences against parasitic females and eggs, and reproductive success of the parasite in current and alternative hosts. Alternative hosts did not discriminate against screaming cowbird females or eggs. Egg survival and hatching success were similarly high in current and alternative hosts, but the survival of parasitic chicks was significantly lower in alternative hosts. Our results indicate that screaming cowbirds have the potential to colonize novel hosts, but higher reproductive success in the current host may favour host fidelity.

Keywords: antiparasitic defences; brood parasitism; host specialization; screaming cowbird; *Molothrus rufoaxillaris*

1. INTRODUCTION

Obligate avian brood parasites show dramatic variation in the degree to which they are host specialists or host generalists (Davies 2000; Sorenson & Payne 2002). The parasitic cowbirds (*Molothrus* spp.) are particularly interesting in this regard, as they vary greatly in the extent of host specificity (Lanyon 1992; Ortega 1998). The basal species of this clade, the screaming cowbird (*Molothrus rufoaxillaris*), is one of the most specialized brood parasites as it has only three known hosts over its entire range in southern South America (Ortega 1998). One of these species, the bay-winged cowbird (*Agelaioides badius*) is largely its main host (Friedmann 1929; Sick 1985; Fraga 1998). By contrast, the two most recently derived species of the clade, the shiny cowbird (*Molothrus bonariensis*) and the brown-headed cowbird (*Molothrus ater*) parasitize more than 200 species (Ortega 1998), showing generalized host use at population and individual levels (Alderson *et al.* 1999; Woolfenden *et al.* 2003; Ellison *et al.* 2006; but see Mahler *et al.* 2007).

The order in which each cowbird species branched off from the rest of its linage correlates with the number of hosts it uses (Lanyon 1992). This has led to the conclusion that the high host selectivity shown by screaming cowbirds was the ancestral character in cowbirds, from which an increasing generalization in host use has evolved (Lanyon 1992). This conclusion, based on parsimony, was criticized by some authors who argued that the current number of hosts is not a dichotomous and genetically determined character, but an evolutionary labile trait that depends more on the ecological circumstances the parasite faces than on its phylogenetic history (Cruz *et al.* 1989, 1998; Rothstein *et al.* 2002). From this perspective, the extreme host specialization exhibited by screaming cowbirds seems puzzling, as this parasite coexists with several species of potentially suitable hosts (Mason 1980).

Why does the screaming cowbird not parasitize more hosts? A possible answer is that suitable hosts that are currently not parasitized have well-developed defences against screaming cowbird parasitism, namely the recognition and rejection of parasitic females or eggs (Mason 1980). According to coevolutionary theory, the reproductive losses posed by parasitism favour the evolution of defences in host populations. In turn, parasites evolve adaptations that counteract host defences (e.g. rapid egg laying and mimetic eggs or chicks; Davies & Brooke 1989; Rothstein 1990; Lotem & Rothstein 1995; Langmore *et al.* 2003). Genetic constraints would not allow parasites to simultaneously maintain specific counteradaptations for each species they parasitize (e.g. different mimetic eggs). A decrease in the number of hosts they use as time passes and more potential hosts evolve effective defences is expected (Rothstein *et al.* 2002). This hypothesis is well supported by data on host use by the common cuckoo (*Cuculus canorus*), which has several female host races,

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each specialized in a particular host and laying a distinctive egg morph that tends to match host eggs (Brooke & Davies 1988; Mosknes & Røskaft 1995; Marchetti *et al.* 1998; Gibbs *et al.* 2000). Host selection by the generalist brown-headed cowbird also appears to be influenced by host defences against parasitic females (Briskie *et al.* 1990; Cruz *et al.* 1990) or eggs (Sealy & Bazin 1995). Likewise, screaming cowbirds may avoid currently parasitizing host species that have evolved effective defences against parasitism. Currently, unused hosts could have defences against screaming cowbirds if interactions between them occurred in the past (Peer & Bollinger 1997; Arias de Reyna 1998; Rothstein 2001; but see Soler *et al.* 2003), or if they evolved antiparasitic defences in response to other brood parasites (i.e. shiny cowbirds) that also serve to protect them against screaming cowbirds (Rothstein *et al.* 2002).

Host specificity can also be maintained if the parasite's reproductive success in currently unused host species is lower than that in the primary host (Fraga 1998). This can occur even in the absence of host discrimination against parasite adults, eggs or chicks, if predation rates in nests of alternative hosts are higher than in those of the primary host (Avilés *et al.* 2006), or if unsuitable parental care or competition with host chicks reduce the parasite's hatching success or chick survival in nests of alternative hosts (Scott & Lemon 1996; Peer & Bollinger 1997; Lichtenstein 1998). Interspecific competition with the sympatric shiny cowbird could also reduce the screaming cowbird's reproductive success in alternative hosts, as has been proposed for other parasitic species that share secondary hosts (Brooker & Brooker 1989; Brooker *et al.* 1990).

The two hypotheses outlined above ultimately predict a lower reproductive success for screaming cowbirds in alternative hosts, but for different reasons: in the first case (coevolutionary hypothesis), it would result from the presence of host defences, while in the second case, the low success would arise due to factors other than host defences, such as differential predation rates, inadequate parental care or competition (either with the host or with shiny cowbird chicks). Our aim of this study was to experimentally test these alternative hypotheses using two unparasitized, but potentially suitable hosts of screaming cowbirds: the chalk-browed mockingbird (*Mimus saturninus*) and the house wren (*Troglodytes aedon*). These species are abundant and widely distributed across the geographical range of screaming cowbirds, breed in the same habitats and partially overlap their breeding seasons with the primary host of screaming cowbirds. In addition, both species are regular and effective hosts of the sympatric shiny cowbird (frequency of parasitism: 60–80%), whose chicks closely resemble screaming cowbird chicks in diet and body size (Fraga 1985; Tuero *et al.* 2007). Chalk-browed mockingbirds are larger than screaming cowbirds (approx. 75 versus 45–50 g, respectively) and breed in open nests, while house wrens are smaller than the parasite (approx. 12 g) and nest in cavities. These species are at the extremes of the range of body sizes of shiny cowbird's hosts (and probably the range of body sizes of potential screaming cowbird's hosts).

If potential alternative hosts are not parasitized because they have developed defences that screaming cowbirds cannot counteract (coevolutionary hypothesis), then chalk-browed mockingbirds and house wrens should be more responsive towards screaming cowbird females or eggs than to those of the shiny cowbird, the species that often parasitizes them. Alternatively, if potential alternative hosts are not parasitized because screaming cowbird's reproductive success in their nests is lower than in those of the primary host (differential success hypothesis), we expect higher egg survival, hatchability and/or chick survival in nests of bay-winged cowbirds than in those of house wrens or chalk-browed mockingbirds.

2. MATERIAL AND METHODS

(a) *Study area and data collection*

The study was conducted at reserve 'El Destino', near the town of Magdalena (35°08′ S, 57°23′ W), in the province of Buenos Aires, Argentina, between 2003 and 2006. The study site is a flat area of marshy grassland, with implanted pastures and old and second growth woodland stands dominated by *Celtis tala* (tala) and *Scutia buxifoli*a (coronillo).

We looked for bay-winged cowbird, chalk-browed mockingbird and house wren nests during each breeding season (November–February), using host behaviour and alarm calls to locate nesting sites. Chalk-browed mockingbirds build large open nests that are typically located in shrubs or trees with dense foliage. Bay-winged cowbirds usually reuse or usurp closed or domed nests built by other species, and occasionally breed in nest boxes (Fraga 1998). House wrens nest in a wide variety of cavities including nest boxes (Tuero *et al.* 2007). To facilitate data collection, we placed wooden nest boxes along the woodlots of our study area. Approximately 20% of bay-winged cowbird and 100% of house wren nests occurred in them. Nests were checked daily or every 2 days until they fledged chicks or failed. For each nest, we recorded initiation date (i.e. date of laying of the first host egg) and in each subsequent visit, the number of host and parasite (screaming or shiny cowbird) eggs or chicks. We marked every egg or chick with waterproof ink for identification as soon as it appeared.

(b) *Defences against screaming cowbirds*

To study host antiparasitic defences, we presented nesting chalk-browed mockingbirds ($n=18$ nesting pairs), house wrens ($n=18$ nesting pairs) and bay-winged cowbirds ($n=24$ nesting pairs), three dummy models, namely female screaming cowbird, female shiny cowbird and female white-browed blackbird *Sturnella superciliaris*. The latter species was used as control because in our study area, it is sympatric with the three hosts, it is similar to screaming and shiny cowbird females in shape and size, and it poses no threat to host nests (Grim 2005). The models used were taxidermic mounts in a life-like position.

In each experimental nest, we presented the three model types sequentially during the laying stage (i.e. when cowbirds represent the greatest danger to the hosts; Hobson & Sealy 1989). The presentation order of models was counterbalanced between nests. We attached the models to a branch at a distance of 1 m from the nest, at the same height and facing the nest rim (open nests) or entrance (closed nests). Each trial began when one of the nest owners detected the model and lasted for 5 min or until one of the members of the pair struck down the model. To avoid habituation or positive reinforcement, we presented the different models with a 15 min interval (Sealy *et al.* 1998). We videotaped all the trials for posterior analysis.

We assessed host defences by measuring the following behaviours for both parents combined: (i) aggression rate (frequency of attacks and close passes directed to the model), (ii) approaches (proportion of time at least one member of the pair was perched to less than 0.5 m from the model), and (iii) nest defence (proportion of time spent in the nest). We chose these variables to characterize host responses according to the level of aggressiveness or degree of risk taken (aggression > approach > nest defence), instead of using arbitrary scores or a more subjective categorization (Sealy *et al.* 1998).

We tested for significant differences in host responses between model types using non-parametric Friedman tests, as response variables did not meet the assumptions of normality and homogeneity of variances. We excluded from the analyses those nests where the members of the pair did not respond to any of the models (three breeding pairs of bay-winged cowbirds and five of house wrens).

(c) *Reproductive success in alternative hosts*

We carried out cross-fostering experiments to assess the reproductive success of screaming cowbirds in alternative hosts. We transferred fresh screaming cowbird eggs obtained from multiple parasitized bay-winged cowbird nests to nests of chalk-browed mockingbirds ($n=53$) and house wrens ($n=32$). We added one screaming cowbird egg per nest during host laying. Incubation periods of parasite and host species are as follows: 12 days for screaming cowbirds (Fraga 1998); 13 days for chalk-browed mockingbirds and bay-winged cowbirds (Fraga 1985, 1998); and 15 days for house wrens (Tuero *et al.* 2007). In a few cases, we transferred newly born screaming cowbird chicks to chalk-browed mockingbirds ($n=3$) and house wren ($n=1$) nests that contained same-aged or 1-day younger host chicks. We chose pairs of nests (donor and acceptor) close enough to relocate the screaming cowbird egg or chick in the experimental nest in less than 30 min. To avoid nest desertion by bay-winged cowbirds, we did not remove more than two screaming cowbird eggs during the same day and always replaced the eggs that had been removed with either artificial (plaster eggs coated with acrylic paint to simulate real screaming cowbird eggs) or natural eggs obtained from clutches that had already been deserted. Clutch size in host nests often changed throughout the laying period due to the destruction of parasite or host eggs by shiny cowbird females, which often punctured one or more eggs when visiting host nests (Fiorini & Reboreda 2006; Tuero *et al.* 2007). Because the aim of our experiment was to determine screaming cowbird success in the most realistic conditions that the parasite would face in chalk-browed mockingbird and house wren nests, which include interspecific competition with shiny cowbirds, we did not manipulate clutch size or composition of the experimental nests after placing the screaming cowbird egg. We used 72 bay-winged cowbird nests as control nests, which were parasitized with screaming cowbird eggs during host laying, either naturally ($n=69$) or artificially ($n=3$). We checked experimental and control nests every 1–2 days. During each visit, we recorded the eggs and chicks present in the nest. We individually inspected eggs and chicks to detect the presence of punctures and ectoparasites (larvae of the genus *Philornis*), respectively, and weighed chicks to the nearest 0.5 g using a Pesola spring scale.

For each host, we calculated the rate of nest survival (proportion of the nests that produced at least one fledgling) and the following estimators of screaming cowbird's reproductive success: egg survival (proportion of eggs laid that were present at the end of incubation); hatching success (proportion of eggs present at the end of incubation that hatched); and chick survival (proportion of chicks born that fledged). Egg survival and hatching success were estimated from nests that survived at least until the nestling stage, while chick survival was estimated considering only the nests that were either successful or failed due to causes other than depredation (e.g. high ectoparasite loads).

Most of our control bay-winged cowbird nests naturally received two or more screaming cowbird eggs (47 out of 72 nests were parasitized more than once). To avoid pseudoreplication, we based our estimations of egg survival, hatching success and chick survival on only one screaming cowbird egg or chick per nest. In nests where parasitic eggs were laid on different days, we chose the first egg laid or the first chick born as the 'focal' egg or chick, respectively. If two eggs were laid or two chicks born on the same day, we randomly selected one of them.

To test for differences in the reproductive success of screaming cowbirds in primary and alternative hosts, we compared the observed frequencies of successful and unsuccessful nests, eggs or chicks between the alternative and the primary hosts using contingency chi-squared tests or Fisher's exact tests. Each parameter of reproductive success was analysed separately.

(d) *Ethical considerations*

Cross-fostering experiments involving permanent translocation of parasite eggs were necessary to assess the screaming cowbird's reproductive success with hosts other than bay-winged cowbirds. Although we did not know *a priori* what the result of these experiments would be, we became aware that cross-fostered chicks experienced higher mortality rates in experimental nests as the study progressed. To avoid the unnecessary loss of screaming cowbird chicks, we reduced our sample sizes to a minimum required for statistical analyses, taking into account that nearly 75% of parasitized nests at our study site typically fail due to depredation or desertion by the host.

3. RESULTS

(a) *Defences against screaming cowbirds*

Bay-winged cowbirds responded more aggressively towards the screaming cowbird than the control model (Friedman test: $\chi^2_2=12.25$, $p=0.002$, $n=21$, *post hoc* comparison $p<0.05$). The aggression rate towards shiny cowbird model was intermediate but not statistically different from those of the other two models (*post hoc* comparison $p>0.1$; table 1*a*). Chalk-browed mockingbirds showed statistically different aggression rates towards the three models (Friedman test: $\chi^2_2=5.93$, $p=0.05$, $n=18$), but *post hoc* comparisons were not statistically significant ($0.05<p<0.1$). House wrens attacked the shiny cowbird model in 6 out of 13 nests tested, but they never responded aggressively towards screaming cowbird or control models (Friedman test: $\chi^2_2=12.0$, $p=0.003$, $n=6$).

Similarly, bay-winged cowbirds approached the screaming cowbird model more often and spent a greater proportion of time close to it than to the control model (Friedman test: $\chi^2_2=14.15$, $p<0.001$, $n=21$, *post hoc* comparison $p<0.05$; table 1*b*). The response towards the shiny cowbird model was intermediate and did not differ

Table 1. Behavioural responses of bay-winged cowbirds ($n=21$ nesting pairs), chalk-browed mockingbirds ($n=18$ nesting pairs) and house wrens ($n=13$ nesting pairs) towards screaming cowbird, shiny cowbird and control species models presented close to their nests during laying. (Values are mean ± s.e. Different superscripts within a row indicate significant differences in host responses among model types (*post hoc* comparisons $p<0.05$, after Friedman tests).)

		model type		
response variable		screaming cowbird	shiny cowbird	control
(*a*) aggression rate (attacks per minute)	bay-winged cowbird	0.69 ± 0.23^{a}	0.35 ± 0.16^{ab}	0.11 ± 0.05^{b}
	chalk-browed mockingbird	0.49 ± 0.28^{a}	1.01 ± 0.30^{a}	0.88 ± 0.39^{a}
	house wren	0^{a}	0.14 ± 0.05^{b}	0^{a}
(*b*) approach to model (% of time)	bay-winged cowbird	50.7 ± 7.7^{a}	32.9 ± 7.5^{ab}	13.9 ± 5.5^{b}
	chalk-browed mockingbird	8.1 ± 2.7^{a}	15.4 ± 4.4^{a}	12.0 ± 5.1^{a}
	house wren	0.2 ± 0.1	1.3 ± 1.1	0
(*c*) nest defence (% of time)	bay-winged cowbird	3.2 ± 2.2^{a}	1.7 ± 1.3^{a}	4.8 ± 3.4^{a}
	chalk-browed mockingbird	0	0	0
	house wren	5.9 ± 4.9^{a}	1.5 ± 1.5^{a}	15.4 ± 9.1^{a}

from the other two models (*post hoc* comparison $p>0.1$). Chalk-browed mockingbirds spent a similar proportion of time close to the screaming cowbird model compared with shiny cowbird and control models (Friedman test: $\chi^2_2=1.58$, $p=0.45$, $n=18$). House wrens rarely (4 out of 13 nests) perched close to the models, thus sample size was too small for statistical analysis.

Nest defence in bay-winged cowbirds and house wrens did not differ among models (Friedman tests: $\chi^2_2=0.38$, $p=0.83$, $n=21$, and $\chi^2_2=2.0$, $p=0.37$, $n=13$, respectively). Chalk-browed mockingbirds never entered the nest during the experiment, regardless of the model type presented (table 1*c*).

(b) *Reproductive success in alternative hosts*

Nest survival differed among hosts (chi-squared test: $\chi^2_2=8.22$, $p=0.02$). It did not differ between chalk-browed mockingbirds and bay-winged cowbirds (mockingbirds, 19/56 nests; bay-winged cowbirds, 19/72 nests; chi-squared test: $\chi^2_1=0.86$, $p>0.05$), but it was higher in house wrens than in the other two hosts combined (18/33 versus 38/128 nests; chi-squared test: $\chi^2_1=7.87$, $p<0.05$; figure 1*a*). The main causes of nest failure were depredation and desertion following multiple parasitism or egg punctures by screaming (in bay-winged cowbird nests) or shiny (in chalk-browed mockingbird and house wren nests) cowbirds.

Chalk-browed mockingbirds and house wrens did not reject screaming cowbird eggs or desert the nest after artificial parasitism. Egg survival of screaming cowbirds did not differ significantly between bay-winged cowbird and house wren nests (31/31 versus 20/22 eggs survived, respectively; Fisher's exact test: $p=0.17$; figure 1*b*), and between bay-winged cowbirds and chalk-browed mockingbirds (31/31 versus 19/22 eggs survived, respectively; Fisher's exact test: $p=0.07$). All egg losses in chalk-browed mockingbird and house wren nests were attributable to punctures produced by shiny cowbirds that visited experimental nests.

Hatching success of screaming cowbird eggs did not differ between nests of bay-winged cowbird and chalk-browed mockingbird (26/31 versus 14/19 eggs hatched, respectively; Fisher's exact test: $p=0.47$), and between nests of bay-winged cowbird and house wren (26/31 versus 14/20 eggs hatched, respectively; Fisher's exact test: $p=0.30$; figure 1*c*).

The survival of screaming cowbird chicks was significantly lower in nests of chalk-browed mockingbird than in those of bay-winged cowbird (3/12 versus 13/14 chicks survived, respectively; Fisher's exact test: $p=0.0008$). In chalk-browed mockingbird nests, screaming cowbird chicks died within few days after hatching mainly as the result of starvation, sometimes combined with parasitism by botfly larvae *Philornis seguyi* (Muscidae, Diptera). Screaming cowbird chicks starved in all mockingbird nests where they coexisted with three or more chicks, but they grew normally and successfully fledged in nests with only one or two nestmates (the number of nestmates in mockingbird nests: 3.1 ± 0.4, range 1–5, $n=12$). One of the nests where the screaming cowbird chick fledged also produced one shiny cowbird fledgling. From the nine nests where the screaming cowbird chick died, four had only host chicks and five had mixed broods with both host and shiny cowbird chicks.

Similarly, screaming cowbird chicks tended to suffer higher mortality in house wren than that in bay-winged cowbird nests (6/11 versus 13/14 chicks survived, respectively; Fisher's exact test: $p=0.06$; figure 1*d*). Chick mortality of screaming cowbirds in house wren nests was in all cases the result of high infestation rates with larvae of botflies. Two house wren nests had screaming and shiny cowbird chicks. In one of these nests, the screaming cowbird successfully fledged while in the other, both chicks died as a result of botfly infestation.

All but one screaming cowbird chicks survived until independence in bay-winged cowbird nests (the number of nestmates in bay-winged cowbird nests: 4.1 ± 0.4, range 1–7, $n=14$). The only death of a screaming cowbird chick occurred in a nest that suffered total brood lost due to an unusually high infestation rate with red mites (*Ornithonyssus iheringi*, Dermanyssidae), an ectoparasite that is relatively common in bay-winged cowbird nests. Four out of thirteen successful bay-winged cowbird nests fledged a shiny cowbird chick along with the screaming cowbird.

Considering the four parameters of reproductive success combined (i.e. nesting success × egg survival × hatching success × chick survival), the probability that a screaming cowbird egg laid in nests of chalk-browed mockingbirds, house wrens and bay-winged cowbirds resulted in a fledgling was 0.05, 0.21 and 0.19, respectively.

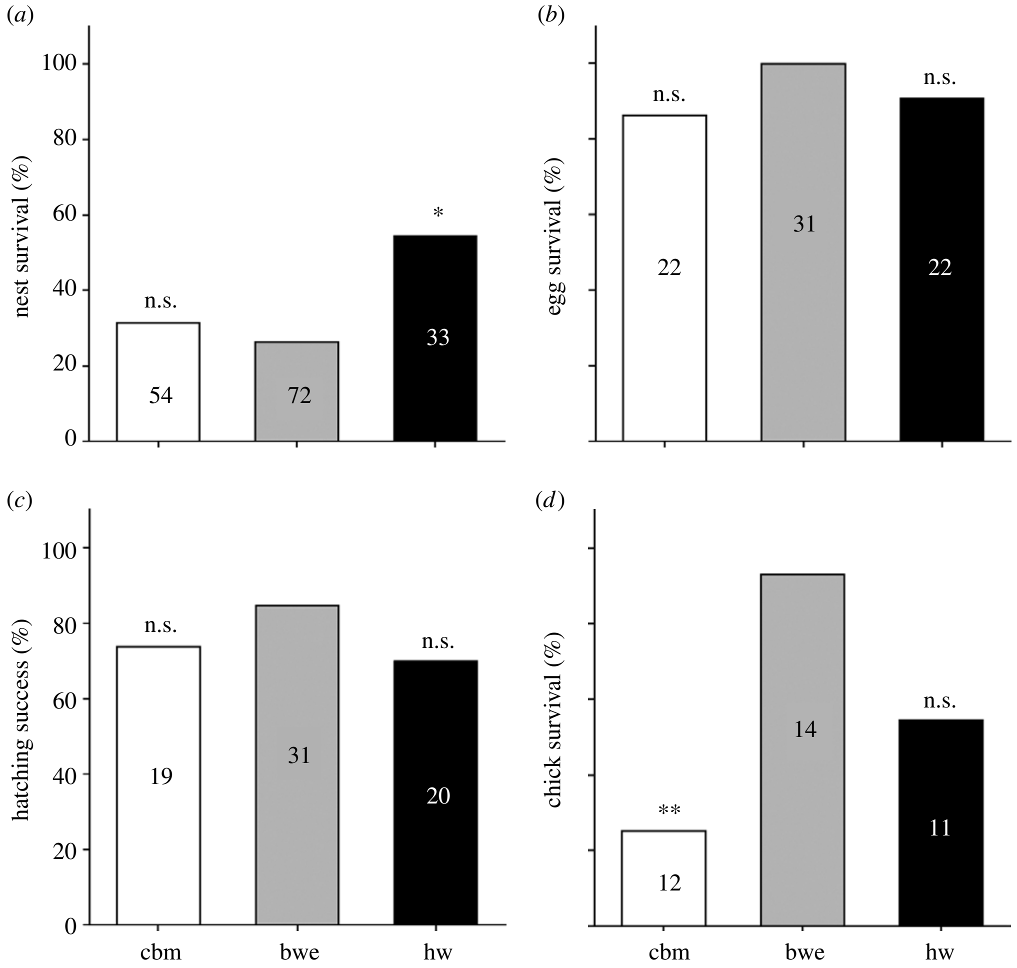

Figure 1. (*a*) Nesting success, (*b*) egg survival, (*c*) hatching success and (*d*) chick survival of screaming cowbirds in experimentally parasitized nests of chalk-browed mockingbirds and house wrens (alternative hosts) compared with that in control nests of its primary host, the bay-winged cowbird. Figures in the centre of bars indicate the number of nests. Asterisks indicate significant differences between experimental and control nests at $^{*}p<0.05$ or $^{**}p<0.01$. n.s., non-significant differences at $p<0.05$.

4. DISCUSSION

Our results indicate that the absence of screaming cowbird parasitism in two currently unused, but potentially suitable hosts cannot be explained by the presence of well-developed defences against parasitic females or eggs. Chalk-browed mockingbirds and house wrens were less aggressive towards screaming than shiny cowbirds (i.e. the species that usually parasitizes them), and only bay-winged cowbirds consistently attacked the screaming cowbird model. Interestingly, our experiment revealed fine-tuned parasite recognition in the three host species, as they showed higher level of responses towards the species that currently represents the highest risk of parasitism (see also Honza *et al.* 2006). As regards egg recognition, neither chalk-browed mockingbirds nor house wrens rejected screaming cowbird eggs, consistent with an earlier report (Mason 1980). Thus, our results did not support the coevolutionary hypothesis to explain why these potential hosts are not parasitized at present by screaming cowbirds.

There are two possible explanations for the lack of specific defences against screaming cowbirds in chalk-browed mockingbirds and house wrens. First, it is possible that these hosts coevolved with screaming cowbirds in the past, and secondarily lost their antiparasitic defences after the parasite shifted away, as has been suggested for other host–parasite systems (Brooke & Davies 1988; Rothstein 1990; Soler *et al.* 1998; but see Rothstein 2001). Alternatively, it is also plausible that the hosts never interacted with screaming cowbirds in the past, and therefore they never evolved antiparasitic defences against screaming cowbirds. We cannot differentiate between these two alternatives but, regardless of the evolutionary pathway that led to the lack of defences observed today, the consequences are the same: both hosts would be at present susceptible to screaming cowbird parasitism, but they are not parasitized.

Our results provide evidence of a lower reproductive success of screaming cowbirds in nests of the alternative host than in those of the primary host. Although egg punctures were more frequent in nests of chalk-browed mockingbirds and house wrens than in nests of bay-winged cowbirds (Fiorini & Reboreda 2006; Tuero *et al.* 2007, this study), we did not find significant differences in survival and hatchability of screaming cowbird eggs between hosts. Thus, our results provide weak support for the hypothesis that host specialization is the result of interspecific competition between parasitic females via the selective destruction of heterospecific parasite eggs when visiting host nests, as suggested for Australian cuckoo species of the genus *Chrysococcyx* sp. (Brooker *et al.* 1990). However, this study provides experimental evidence that screaming cowbird chicks reared in nests of alternative hosts have lower survival rates than those in nests of the primary host. In most experimental chalk-browed mockingbird nests, screaming cowbird chicks suffered from intense competition for food with their nestmates and starved despite always being born before the other chicks. Starvation of the screaming cowbird chick occurred in both broods with only host chicks and mixed broods that also contained a shiny cowbird chick, thus further experimental manipulations are needed to assess whether competition with shiny cowbirds increases the risk that screaming cowbirds are outcompeted for food. Interestingly, the survival rate of screaming cowbird chicks was lower than that reported for shiny cowbirds in nests of chalk-browed mockingbirds with similar brood sizes (0.25 versus 0.62–0.79; Sackmann & Reboreda 2003; Fiorini *et al.* 2005, this study), which suggests that the two cowbird species actually differ in their competitive abilities under these conditions. Although interspecific competition has been invoked as a major selective force driving specialization and segregation in host use in avian brood parasites (Brooker *et al.* 1990; Davies 2000), there are very few studies in the literature on competitive interactions between sympatric avian brood parasites. Non-evicting parasites, such as the screaming and shiny cowbird, which are broadly sympatric in southern South America and similar in morphology, provide an excellent model for investigating interspecific competition in more detail.

In house wren nests, the survival of screaming cowbird chicks was marginally lower than that in bay-winged cowbird nests due to heavy infestations with botfly larvae *P. seguyi*. Again, survival rate was lower than that reported for shiny cowbirds parasitizing the same host in nest boxes (0.55 versus 0.90; Fiorini *et al.* 2005). This difference can be partially explained by variation in timing of breeding between the two parasites as the incidence of botfly parasitism in our study area increased through December and January (Rabuffetti & Reboreda 2007), coincidently with the start of the breeding season of screaming and bay-winged cowbirds. Botflies do not affect the growth and survival of screaming cowbird chicks in bay-winged cowbird nests because this host removes the larvae from the chicks (both parasitic and their own), usually within 24–48 h after they are infested (Fraga 1984; M. C. D. Mársico 2005 and 2006, personal observation). Shiny cowbirds start to breed in October, and therefore do not suffer from heavy infestations with botflies until late in the season.

In bay-winged cowbird nests, screaming cowbirds had high fledging success, even in those nests that were also parasitized by shiny cowbirds. Competition for food is likely to be less intense in this host than that in alternative hosts, as most breeding pairs have one or more helpers at the nest that contribute to chick provisioning (Fraga 1991). Although breeders, and particularly females, often reduce their parental effort in avian cooperatively breeding groups, the overall nestling feeding rates usually increase with group size (Hatchwell 1999; MacColl & Hatchwell 2003; Woxvold *et al.* 2006), and helpers' contribution may fully compensate for initial reductions in maternal investment (Russell *et al.* 2007). Remarkably, the other two known screaming cowbird hosts, the chopi blackbird (*Gnorimopsar chopi*; Fraga 1996) and the brown-and-yellow marshbird (*Pseudoleistes virescens*; Mermoz & Reboreda 1996), are also cooperative breeders (Orians *et al.* 1977; Mermoz & Fernández 2003), which indirectly reinforces the idea that competition for food with nestmates may be critical for screaming cowbirds.

Despite the higher survival of screaming cowbird chicks in nests of its primary host, the differences in reproductive success between primary and alternative hosts become smaller when we take into account nest survival. In this case, the percentage of screaming cowbird eggs that result in fledglings in mockingbird, bay-winged cowbird and house wren nests is 5, 19 and 21, respectively. High rates of nest predation and abandonment of heavily parasitized clutches in bay-winged cowbirds dilute the parasite's expectation of success. Indeed, overall reproductive success in the primary host is slightly lower than that in house wrens, although nest survival in the latter host is probably overestimated owing to lower predation rates in nest boxes (Purcell *et al.* 1997). Therefore, although high survival of screaming cowbirds in bay-winged cowbird nests may favour host specificity (Fraga 1998), it does not fully explain why they do not parasitize a broader range of hosts.

To explain host specificity in other brood parasites, it has been hypothesized that a mechanism of imprinting favours host specialization. According to this hypothesis, the young parasite learns some features of the foster parents or the nest or habitat where it was reared, and later seeks the same host, nest type or habitat to lay its eggs (Mosknes & Røskaft 1995; Teuschl *et al.* 1998; Payne *et al.* 2002; Langmore & Kilner 2007). This mechanism may result in host-specific matrilineal lineages. Although we did not test host imprinting in screaming cowbirds, our results are consistent with the hypothesis of a rooted host preference in this parasite. Preferences for a nest or habitat type are unlikely because bay-winged cowbirds breed in a wide variety of closed nests (including cavities) and share their habitat with many other passerines that can be suitable cowbird hosts. Screaming cowbirds have a prolonged association with adult and juvenile bay-winged cowbirds after leaving the nest (Fraga 1998), and adults of both species often forage in mixed flocks throughout the year and share roosting sites (M. C. D. Mársico & J. C. Reboreda 2004, personal observation), thus providing screaming cowbirds with broad opportunities to imprint on bay-winged cowbirds.

Other highly specialized avian brood parasites have been able to colonize new species apart from their main host. In the host-specific parasitic indigobirds (*Vidua* spp.), misimprinting or egg-laying mistakes presumably caused host shifts that led to new host–parasite associations and sympatric speciation in the parasites (Payne *et al.* 2000, Sorenson *et al.* 2003). In some cuckoo species, flexibility in host preference or a combination of host and habitat preferences allows parasites to use secondary hosts if the primary host is spatially or temporally unavailable (Langmore & Kilner 2007). Both possibilities are compatible with the observed pattern of host use in screaming cowbirds, and further studies are necessary to disentangle the cues involved in host choice and maintenance of host preferences in this brood parasite.

The experiments performed in this work comply with the current laws of Argentina.

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