

High frequency but low impact of brood parasitism by the specialist Screaming Cowbird on its primary host, the Baywing

María C. De Mársico^{A,B} and Juan C. Reboreda^A

^ADepartamento de Ecología, Genética y Evolución, and IEGEBA-CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA Buenos Aires, Argentina.

^BCorresponding author. Email: de_marsico@ege.fcen.uba.ar

Abstract. Brood-parasitic cowbirds (*Molothrus* spp.) exploit the parental care of other species (hosts) that raise their offspring. Parasitism by cowbirds reduces host reproductive success in several ways and quantifying such costs is an important step to better understand evolutionary interactions in host–parasite associations. We estimated the costs of parasitism by the host-specialist Screaming Cowbird (*M. rufoaxillaris*) to the reproductive success of its primary host, the Baywing (*Agelaioides badius*). We tested the effect of Cowbird parasitism on egg survival, hatching success, nestling survival and body mass at fledging of Baywings in a population of eastern Argentina where the frequency of parasitism by Screaming Cowbirds exceeds 90% of Baywing nests. Egg survival decreased with the number of Screaming Cowbird eggs laid during the egg-stage and, on average, host clutch-size was reduced by 10% per parasitic event. However, contrary to our expectations, we did not find any clear effect of parasitism on hatching success, nestling survival and body mass at fledging of Baywings. Our results suggest that, despite its high frequency, parasitism by Screaming Cowbirds has a rather little effect on the viability of Baywing offspring. We discuss how clutch rejection behaviour and flexible nest-provisioning rules of the hosts might help to explain this paradoxical result.

Additional keywords: Baywing, brood parasitism, host use, *Molothrus*, reproductive success.

Received 20 January 2014, accepted 26 May 2014, published online dd mmm yyyy

Introduction

Brood-parasitic cowbirds (Icteridae: *Molothrus* spp.) lay their eggs in the nests of other species (hosts), which provide all parental care to the parasitic offspring. Unlike other obligate brood parasites, such as most Old World cuckoos (Cuculinae), New World cuckoos (Neomorphinae) and honeyguides (Indicatoridae), cowbird hatchlings do not actively evict or kill the host offspring, but are usually reared in mixed broods alongside host young (Ortega 1998; Robinson and Rothstein 1998; Davies 2000). Yet cowbird parasitism can reduce reproductive success of hosts in several ways, including the removal or puncturing of host eggs by parasitic females during visits to nests (Carter 1986; Sealy 1992; Peer 2006; Gloag *et al.* 2012), increased hatching failure of host eggs (Burhans *et al.* 2000; Hoover 2003; Tuero *et al.* 2007), increased mortality of host nestlings owing to competition with cowbird young (Dearborn *et al.* 1998; Payne and Payne 1998; Hoover 2003; Hoover and Reetz 2006; Rasmussen and Sealy 2006), reduced post-fledging survival of host young (Payne and Payne 1998; Hoover and Reetz 2006; but see Smith 1981), and increased risk of desertion or depredation of parasitised broods (Payne and Payne 1998; Dearborn 1999; Burhans *et al.* 2000; Hosoi and Rothstein 2000; Smith *et al.* 2003; De Mársico and Reboreda 2010). Besides these potential

effects on nest productivity, parasitism by cowbirds may have consequences for host demography if rearing parasitised broods decreases the chances of survival or future reproduction of host parents (Hoover and Reetz 2006; but see Payne and Payne 1998), or if competition with cowbird nestlings results in sex-biased mortality of host offspring (Zanette *et al.* 2005).

The effect of cowbird parasitism can vary considerably between host species but it is more severe when parasitic nestlings are larger or hatch earlier than host young (Lorenzana and Sealy 1999; Hauber 2003). Many small hosts of the Brown-headed Cowbird (*M. ater*) seldom fledge any of their own young from parasitised nests (recently reviewed in Peer *et al.* 2013), which may result in fitness costs comparable to those imposed by 'nest-mate killing' brood parasites. For medium and large hosts with fairly short incubation periods, the major cost of parasitism is usually the loss of one or a few eggs through the destruction of eggs by female cowbirds because the viability of their offspring is likely to be little affected by the presence of parasitic eggs and nestlings in the brood (Eckerle and Breitwisch 1997; Clotfelter and Yasukawa 1999; Sackmann and Reboreda 2003; Astié and Reboreda 2006). However, the effect of parasitism in medium and large hosts can be greater if hosts are regularly parasitised multiple times (e.g. Trine 2000; Duré Ruiz *et al.* 2008). Given that the costs

of parasitism are a major determinant of the strength of selection for anti-parasite defences in host populations, quantifying such costs at different stages of the nesting cycle appears as a fundamental step to understand better the evolutionary interactions between, and population dynamics of, cowbirds and their hosts (May and Robinson 1985; Lotem and Nakamura 1998; Spottiswoode *et al.* 2012).

In this study we assess the effect of parasitism by the most specialised of the cowbird species, the Screaming Cowbird (*M. rufoaxillaris*), on the reproductive success of its primary host, the Baywing (Icteridae: *Agelaioides badius*). The Screaming Cowbird almost exclusively parasitises the Baywing, although it uses two other other icterine species as secondary hosts at some localities (Sick 1985; Fraga 1996; Mermoz and Reboreda 1996). The frequency of parasitism of Baywings by Screaming Cowbirds is extremely high (range 83–100%) and most nests are parasitised multiple times (Hoy and Ottow 1964; Fraga 1998; De Marsico *et al.* 2010). The intensity of parasitism (i.e. mean number of parasite eggs per parasitised nest) ranges from three to five, but any single Baywing nest may receive up to 19 parasite eggs (Hoy and Ottow 1964; Fraga 1998). Screaming Cowbird females lay their eggs before dawn, but they make ‘non-laying’ visits to Baywing nests throughout the day (M. C. De Marsico *et al.*, unpubl. data). The Baywing is also a host of the Shiny Cowbird (*M. bonariensis*), but rates of parasitism by this species are much lower (16–23%; Fraga 1998; De Marsico *et al.* 2010). Baywings almost invariably evict the whole parasitised clutch from the nest, including their own eggs, when it is twice or more the modal host clutch-size of four eggs, but they typically incubate clutches containing from one to three cowbird eggs (De Marsico *et al.* 2013). Screaming Cowbirds are larger in body mass than Baywings (adult body mass of Screaming Cowbirds, 50–60; of Baywings, 40–50 g; Fraga 1998) and have a shorter incubation period (12 cf. 13 days; Fraga 1998; De Marsico *et al.* 2010). Thus, when parasitism occurs during the laying period of the host, the Cowbird nestlings have a head-start in the competition for food delivered by host parents. Prior studies indicate that multiple parasitism by Screaming Cowbirds increases the likelihood of nest desertion or clutch rejection by Baywings (Fraga 1998; De Marsico and Reboreda 2010; De Marsico *et al.* 2013) but the effect of multiple parasitism on the viability of the eggs and nestlings of the hosts has not yet been quantified.

Parasitism by Screaming Cowbirds may decrease the success of host offspring in several ways. Firstly, adult Screaming Cowbirds are known to puncture host eggs during nest visits (Hoy and Ottow 1964; Fraga 1998) and it is expected that host egg survival will decrease with the intensity of parasitism (i.e. a surrogate of rate of nest visitation). Secondly, multiple parasitism may increase the risk of hatching failures by lowering the incubation efficiency of host eggs. Finally, it is expected that survival of host nestlings or body mass at fledging will be negatively related to the number of parasitic nestlings in the brood because larger and older Cowbird nestlings strongly compete for food with host young and may increase the likelihood of brood reduction (Dure Ruiz *et al.* 2008). We tested these predictions by analysing the effect of the intensity of Screaming Cowbird parasitism on the probability of survival of host eggs, hatching success and nestling survival, and on body mass at

fledging of host young in a Baywing population from eastern Argentina.

Materials and methods

Study site and data collection

The study was conducted at the private reserve ‘El Destino’, located within the Parque Costero del Sur Biosphere Reserve (MAB-UNESCO, <http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/latin-america-and-the-caribbean/>, accessed 17 June 2014), near the town of Magdalena (35°08’S, 57°23’W), in the province of Buenos Aires, Argentina, during the breeding seasons 2002–07 and 2009–10. The study area comprises ~300 ha of flooding grasslands interspersed with patches of woodland dominated by Tala (*Celtis ehrenbergiana*) and Coronillo (*Scutia buxifolia*). Baywings and Screaming Cowbirds are year-round residents in the area.

Baywings are single-brooded and breed in the study area from late November to mid-February. Parasitism by Screaming Cowbirds occurs throughout the breeding season of the Baywing (De Marsico *et al.* 2010). Baywings seldom build their own nest but breed instead in old domed nests built by other species (e.g. Firewood-gatherer, *Anumbius annumbi*; thornbirds, *Phacellodomus* spp.; spinetails, *Synallaxis* spp.; Rufous Hornero, *Furnarius rufus*; Great Kiskadee, *Pitangus sulfuratus*), holes in trees and nest-boxes (Fraga 1998; De Marsico *et al.* 2010). Nearly 25% of the nests in our sample were in nest-boxes placed in the study area before the beginning of the study (see De Marsico *et al.* 2010 for further details). Baywings are facultative cooperative breeders, with nearly 40% of nests having one to three helpers at the nest and which typically join the breeding pair after young hatch (Fraga 1991; Ursino *et al.* 2011).

We searched thoroughly for Baywing nests within the study area throughout the breeding season. Nests were found along the edges of woodland patches or in isolated trees, at heights of 1.5–7 m above the ground. Collection of data was limited to nests built at a height of up to 5 m, which could be reached with a portable ladder. This sample comprises approximately two-thirds of all nests found and reflects the variety of nest-types used by Baywings. We monitored 202 nests, of which 73 (35%) survived to the nestling stage and 43 (22%) produced at least one host or parasite fledgling. We inspected nests every 1–3 days until the nestlings fledged or the nest failed. In each visit up until nestlings 10–11 days old (see below), we recorded the contents of the nest and individually marked every egg and nestling with a permanent marker. We observed parental activities from a distance of ~10 m afterwards to determine whether the young fledged. Baywing and Screaming Cowbird eggs are very much alike in size and shape (mean length × width: Baywing, 23.6 ± 0.1 × 17.8 ± 0.0; Cowbird, 23.7 ± 0.1 mm × 17.9 ± 0.0 mm; De Marsico *et al.* 2010), but can be identified using diagnostic color and patterns of spotting (Fraga 1983). Nestling and fledgling Screaming Cowbirds are also very similar to Baywing young, but newly hatched nestlings can be distinguished by differences in the colour of the skin and bill (Fraga 1979).

During inspections of nests, we checked every egg for the presence of punctures caused by Cowbirds. Occasionally, we did not find punctured eggs but found one or more eggs missing

along with yolk stains or pieces of eggshell on the surface of the remaining eggs. In such cases, we assumed that the missing egg or eggs had been punctured by Cowbirds and subsequently removed by Baywings during nest sanitation on the basis of videorecordings showing these behaviours (De Mársico *et al.* 2013; see Supplementary material, video recording). Whenever possible, we weighed nestlings daily or every other day to the nearest 0.1 or 0.5 g using 10- and 60-g capacity Pesola spring scales to respectively weigh nestlings up to 10 g (1–2 days old) and from day 3 onwards. We banded them at the age of 10–11 days with a unique combination of coloured plastic bands (A. C. Hughes Ltd., Hampton Hill, UK) and a numbered aluminium band (Porzana Ltd., Icklesham, UK). After that time, we continued to monitor nests from a distance of ~10 m away from the nest daily or every other day in order to determine the fate of the nest and the number of host and Cowbird nestlings fledged.

Data analysis

We tested the effect of Screaming Cowbird parasitism separately on the survival of host eggs, hatching success and nestling survival using generalised linear models (GLM) with binomial error structure and logit link function. We fitted models by the iterated re-weighted least-squares method using the ‘glm’ function in R version 3.0.0 (R Development Core Team 2013). The response variables were egg survival (proportion of host eggs laid that remained intact in the nest by the end of incubation), hatching success (proportion of host eggs at the end of incubation that hatched), and nestling survival (proportion of host hatchlings that fledged). Each one was entered in model analysis as a two-vector response variable comprising the number of ‘successes’ (i.e. number of host eggs that survived or hatched or nestlings that died) and the number of ‘failures’ (i.e. number of host eggs that were damaged or failed to hatch or nestlings that died; Crawley 2007).

We modelled egg survival using only nests that were visited daily during laying by the host and that survived to the nestling stage ($n=40$). This subsample excludes nests found after the host clutch was complete, for which we could not reliably determine host clutch-size and thus the number of eggs that might be punctured. We modelled hatching success using nests found before the end of incubation that survived to the nestling stage ($n=51$). Two nests in which the entire host clutch failed to hatch were excluded from model analysis, as hatching failure in these cases was probably a result of the Baywing females laying infertile eggs. To model nestling survival we used nests found before hatching that survived to fledging ($n=38$). This subsample excludes nests that were depredated during the nestling stage.

Explanatory variables in the model analyses were number of Screaming Cowbird eggs or nestlings (see below), clutch- or brood-size of host, and initiation date of clutch relative to the first host nesting attempt in the season. Screaming Cowbirds can visit Baywing nests throughout the nesting cycle. Therefore, our egg-survival model included the total number of Screaming Cowbird eggs laid over the egg-stage as a surrogate of the minimum number of visits by parasitic females that could have resulted in damage to host eggs. To model the effect of parasitism on hatching success of Baywings, we ran two sets of models: one including the number of Screaming Cowbird eggs laid during the

host laying period and the other one including the number of parasitic eggs laid over the egg-stage in order to account for the potential effects of both early and late parasitism on the incubation efficiency of host eggs. Finally, to model the effect of parasitism on survival of host nestlings we considered only the number of Screaming Cowbird nestlings that hatch before or on the same day as host young, as those hatched after the youngest Baywing nestling are less likely to outcompete host young and often die soon after hatching (Fraga 1998).

To analyse the effect of Screaming Cowbird parasitism on body mass of host young at fledging we first estimated the asymptotic body mass of 89 individual Baywing nestlings that survived at least to the age of 10 days ($n=36$ broods with complete records of nestling weights) using the logistic growth curve: $W(t) = A \div (1 + e^{-K(t-t_1)})$, where $W(t)$ denotes nestling body mass at age t , A is the asymptotic body mass, K is a growth constant, t is nestling age (in days) and t_1 is the age of maximum growth (Ricklefs 1967). We obtained parameter estimates for individual nestlings by fitting daily weights to the logistic growth curve using non-linear least-squares regression in SYSTAT 10.0 (SPSS, Chicago, IL).

To assess the effect of parasitism on body mass at fledging of host nestlings we fitted a linear mixed model (LMM) by maximising the restricted log-likelihood (REML) using the ‘lme’ function in the ‘nlme’ package of R version 3.0.0 (R Development Core Team 2013). The explanatory variables were the number of Screaming Cowbird nestlings hatched synchronously to host young (see above), host brood-size and the relative initiation date of clutch. We included nest identity as a random effect as we measured 2–5 host nestlings per brood. Screaming Cowbird nestlings might induce higher provisioning rates by host parents (Ursino *et al.* 2011), which in turn may result in non-linear effects of parasitism on host body mass. To account for this possibility we included the number of Cowbird nestlings as a linear and quadratic term in the model.

In the GLM and LMM analyses, we first estimated the full model and then sequentially eliminated non-significant terms ($P>0.10$) until a minimal model was obtained. We derived P -values for significant terms from the minimal model, and non-significant P -values by individually reintroducing each non-significant term in the minimal model. All statistical tests were two-tailed.

Results

Baywings suffered losses of eggs attributable to punctures by Cowbirds in nine of 40 (22.5%) nests in our sample, of which one was parasitised only once and eight were parasitised multiple times. Parasitised nests had a mean of 3.3 Screaming Cowbird eggs (s.e. 0.3, range 1–9, $n=35$). We did not detect punctured or missing host eggs in unparasitised nests ($n=5$). Model analysis indicates that survival of host eggs decreased with the number of Screaming Cowbird eggs laid over the egg-stage (GLM: estimate s.e. = -0.25 ± 0.13 , Wald $z = -1.97$, $P = 0.049$; Fig. 1). There was no significant effect of host clutch-size (estimate \pm s.e. = 0.51 ± 0.50 , Wald $z = 1.00$, $P = 0.31$) and relative initiation date of clutch (estimate \pm s.e. = -0.02 ± 0.02 , Wald $z = -1.02$, $P = 0.31$) on survival of host eggs. Host clutch-size at the end of incubation decreased with intensity of parasitism (Spearman rank correla-

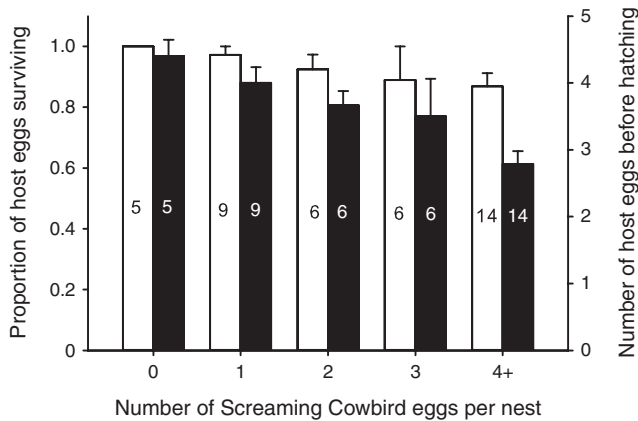


Fig. 1. Proportion of Baywing eggs that survive to hatching (open bars) and number of host eggs remaining in the nest at the end of incubation (black bars) in relationship to the number of Screaming Cowbird eggs laid per nest over the egg-stage (i.e. intensity of parasitism). Values are expressed as means \pm s.e.; sample sizes are given within bars.

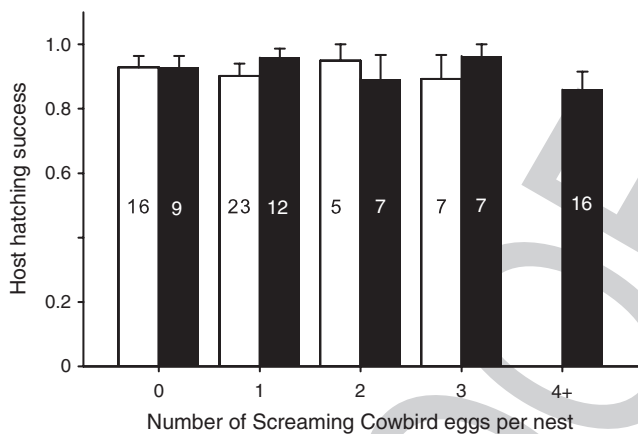


Fig. 2. Hatching success of Baywing eggs in relation to the number of Screaming Cowbird eggs laid per nest during the laying period of Baywings (open bars) and over the entire egg-stage (black bars). Bars represent the mean proportion (\pm s.e.) of host eggs at the end of incubation that hatched. Sample sizes are given within bars.

tion: $\rho = -0.62$, $P < 0.0001$, $n = 40$ nests; Fig. 1). On average, Baywings lost 0.11 ± 0.04 eggs per parasitic event.

Hatching failures of host eggs occurred at 13 of 51 (25%) nests that survived to the nestling stage, including three of nine unparasitised nests, two of 12 singly parasitised nests, and eight of 30 multiply parasitised nests. Mean intensity of parasitism was 3.1 cowbird eggs per clutch (s.e. 0.3, range 1–9, $n = 42$ nests) considering all parasitic eggs laid over the egg-stage, and 1.5 eggs per clutch (s.e. 0.1, range 1–3, $n = 35$) considering only the parasitic eggs laid synchronously with laying by the host. Model analysis showed no significant effect on hatching success of Baywing eggs of the number of Cowbird eggs laid during the Baywing laying period (GLM: estimate \pm s.e. = -0.24 ± 0.25 , Wald $z = -0.94$, $P = 0.35$) and over the egg-stage (estimate \pm s.e. = -0.08 ± 0.12 , Wald $z = -0.62$, $P = 0.54$; Fig. 2), host clutch-size (estimate \pm s.e. = -0.21 ± 0.38 , Wald $z = -0.55$,

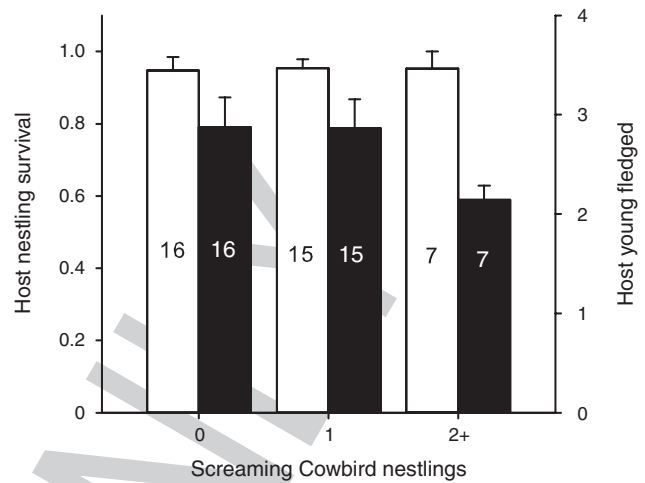


Fig. 3. Proportion of Baywing hatchlings that fledged (open bars) and number of Baywings that fledged (black bars) in nests that had zero, one, or two or more Screaming Cowbird nestlings that hatched synchronously with host young. Values are expressed as means \pm s.e.; sample sizes are given within bars.

$P = 0.58$) and relative initiation date of clutch (estimate \pm s.e. = -0.01 ± 0.02 , Wald $z = -0.32$, $P = 0.75$).

Baywing nestling mortality occurred at six of 38 nests (16%) that survived to the fledging stage, including two of 16 unparasitised nests, three of 15 singly parasitised nests and one of seven multiply parasitised nests. In all cases, only a single Baywing nestling died, usually the youngest in the brood. Mean intensity of parasitism was 1.4 nestlings (s.e. 0.1, range 1–3, $n = 22$), considering only those that hatched synchronously with host young. Model results showed no significant effect on host nestling survival of the number of Screaming Cowbird nestlings (GLM: estimate \pm s.e. = -0.12 ± 0.50 , Wald $z = -0.24$, $P = 0.81$; Fig. 3), host brood-size (estimate \pm s.e. = -0.20 ± 0.42 , Wald $z = -0.48$, $P = 0.63$), and relative initiation date of clutch (estimate \pm s.e. = -0.03 ± 0.02 , Wald $z = -1.23$, $P = 0.22$). The number of host young fledged from Baywing nests was not significantly correlated with the number of parasitic nestlings in the brood (Spearman rank correlation: $\rho = -0.23$, $P = 0.16$, $n = 38$; Fig. 3).

We did not find a significant effect of the number of Screaming Cowbird nestlings in the brood (LMM: linear estimate \pm s.e. = 0.09 ± 1.19 , $F_{1,31} = 0.91$, $P = 0.35$; quadratic estimate \pm s.e. = -0.26 ± 0.46 , $F_{1,31} = 0.31$, $P = 0.58$; Fig. 4), host brood-size (estimate \pm s.e. = 0.38 ± 0.42 , $F_{1,31} = 0.79$, $P = 0.38$) and relative initiation date of clutch (estimate \pm s.e. = 0.01 ± 0.02 , $F_{1,31} = 0.14$, $P = 0.71$) on the estimated body mass at fledging of Baywing young.

Discussion

Our results indicate that parasitism by Screaming Cowbirds decreased the viability of Baywing offspring mainly through reducing the survival of host eggs, which can be attributed to the egg-puncturing behaviour of parasitic female Cowbirds during visits to host nests. In support of this conclusion, the probability of host eggs surviving to hatching and host clutch-size at the end of incubation decreased with the number of Screaming Cowbird

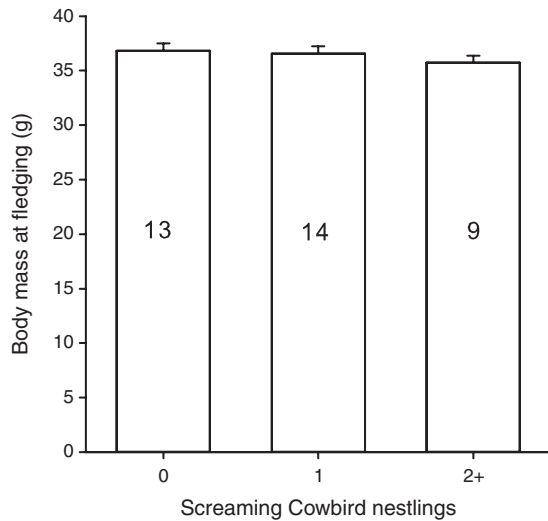


Fig. 4. Mean body mass at fledging (\pm s.e.) of Baywings in relation to the number of Screaming Cowbird nestlings in the brood that hatched synchronously with host young. Sample sizes are given within bars.

eggs laid, which provides a minimum estimate of the frequency of visits to nests by Screaming Cowbird females over the egg-stage. This finding is in agreement with prior studies showing a negative effect of parasitism by cowbirds on survival of host eggs in several host species (Sealy 1992; Massoni and Reboreda 1998; Clotfelter and Yasukawa 1999; Astié and Reboreda 2006; Gloag *et al.* 2012). However, we did not detect egg losses at unparasitised Baywing nests as is expected to occur if parasitic females damage host eggs during both laying and non-laying visits to nests (e.g. Astié and Reboreda 2006; Gloag *et al.* 2012). Given the high prevalence of Screaming Cowbird parasitism in our study population, it is possible that unparasitised nests in our sample went completely undetected by female Screaming Cowbirds. Also, although unparasitised and parasitised Baywing nests were comparable in architecture, location and timing of initiation of clutch, it is possible that they differed in more subtle cues used by female Screaming Cowbirds to decide where to lay, such as host behaviours or nest attributes that signal parental quality. Experiments involving artificial parasitism of unparasitised nests are necessary in order to assess the influence of parental quality on the likelihood of parasitism. Another possibility is that defensive behaviours by Baywings at unparasitised nests were effective enough to prevent female Screaming Cowbirds from puncturing host eggs and laying their own. Video-recording of Baywing nests obtained as part of another study showed that hosts often sit tightly on the nest-cup when Screaming Cowbird females arrive at the nest (De Mársico *et al.* 2013). Although such behaviour does not necessarily preclude laying by parasitic females, it might block their access to the nest contents, thus providing an effective protection for host eggs against parasite attacks (see also Tewksbury *et al.* 2002).

In contrast, the extent of damage to host eggs caused by female Cowbirds may reflect a trade-off between the benefits of reducing competition to the parasitic offspring and the costs of losing assistance to them in stimulating parental care by the host (Kilner *et al.* 2004; Gloag *et al.* 2012). In the Shiny Cowbird there is

evidence that parasitic females from the same population damage fewer host eggs per parasitic event when parasitising the small House Wren (*Troglodytes aedon*) than the large Chalk-browed Mockingbird (*Mimus saturninus*), which can be the result of individual female Shiny Cowbirds within that population preferentially parasitising one of both host species and exhibiting egg-puncturing behaviours adjusted to the preferred host (Mahler *et al.* 2007; Fiorini *et al.* 2009; Tuero *et al.* 2012). Such behaviours seem to be adaptive as Cowbird nestlings reared alongside host young survived better or attained a higher body mass than those reared alone in House Wren nests but not in Chalk-browed Mockingbird nests (Fiorini *et al.* 2009; Gloag *et al.* 2012). The rather low incidence of host egg-losses found in this study (0.11 ± 0.04 host eggs punctured per parasitic event), similar to that reported in House Wrens parasitised by Shiny Cowbirds (0.07 ± 0.03 ; Fiorini *et al.* 2009), indicates that Screaming Cowbirds may also benefit from a reduced virulence towards host eggs in Baywing nests, although this hypothesis requires further study. It is also worthwhile to note that egg-puncturing by Screaming Cowbirds may come at the cost of causing nesting failures, as Baywings are more likely to desert parasitised clutches following repeated damage to eggs (De Mársico and Reboreda 2010). From this perspective, it is possible that the potential benefits of egg-puncturing behaviour to Screaming Cowbird females, such as reducing competition for their offspring or keeping clutch-size below host's rejection threshold (Fraga 1998; De Mársico *et al.* 2013), may be outweighed by the costs of triggering desertion of nests. Such a trade-off would also help to explain the low frequency of egg-punctures observed in Baywing nests.

Contrary to our predictions we did not find a significant effect of parasitism on hatching success of Baywings. Hatching failures of host eggs occurred at approximately the same rate in unparasitised (30%) and multiply parasitised nests (27%), and less frequently at singly-parasitised nests (17%). This result strongly suggests that factors in addition to Screaming Cowbird parasitism might affect the hatching success of Baywing eggs. For instance, at least some Baywing eggs might have failed to hatch because they were infertile or contained non-viable embryos rather than decreased incubation efficiency as a consequence of parasitism. Similarly, model results did not support our prediction that Cowbird parasitism would decrease the survival of Baywing nestlings. Brood-reduction was infrequent during this study and results of model analyses showed no significant effect of the number of Screaming Cowbird nestlings in the brood on both the likelihood of survival of host nestlings and body mass at fledging of host young. These results were unexpected because Screaming Cowbird nestlings that hatch synchronously with host young have the potential to outcompete them for food given the parasite's larger size and more intense begging displays (Lichtenstein 2001; De Mársico *et al.* 2010). It is possible that these results are a consequence of host parents adjusting their parental effort in response to parasitism by Cowbirds. If Screaming Cowbird nestlings are unable to monopolise parental feedings, then an increase in the level of nest-provisioning by hosts may reduce the costs of competition to their offspring at the expense of increasing the costs of current reproduction to the host parents. Various studies have shown that nestlings of other cowbird species (i.e. Brown-headed Cowbird, Shiny Cowbird) begged more intensely

than host young and induced higher levels of parental care (Dearborn *et al.* 1998; Hoover and Reetz 2006; Gloag and Kacelnik 2013; but see Rivers *et al.* 2010). For example, in the Red-winged Blackbird (*Agelaius phoeniceus*), a common host of the Brown-headed Cowbird with facultative biparental care, the presence of a Cowbird nestling in the brood was positively associated with rates of food delivery by females and the probability that males assisted them in nest-provisioning (Grayson *et al.* 2013). In this host species, male parental care enhances nestling growth and nest productivity relative to broods attended by females only (Muldal *et al.* 1986; Yasukawa *et al.* 1990) and thus it is likely to reduce the costs of parasitism to host young (Grayson *et al.* 2013).

In Baywings, there is some evidence that rates of nest-provisioning and the number of helpers recruited increased with the number of Cowbird nestlings in the brood (Ursino *et al.* 2011), which may help to explain why host nestlings survived equally well, and leave the nest in similar body condition, at unparasitised, singly parasitised and multiply parasitised nests. In relation to this, it is worthwhile to note that all three host species known so far for Screaming Cowbirds are cooperative breeders (Orians *et al.* 1977; Fraga 1991, 2008), which suggests a role of increased parental care in driving evolutionary interactions between Screaming Cowbirds and their hosts. However, further studies are needed to determine whether it is host parents or helpers-at-the-nest that pay the costs of increased parental care and to what extent Screaming Cowbirds gain a fitness advantage by preferentially targeting cooperatively breeding hosts (see Canestrari *et al.* 2009; Feeney *et al.* 2013).

It has been recently argued that the virulence of parasitic offspring would be a determinant of the strength of host defences against parasitism (Spottiswoode *et al.* 2012). In Baywings, however, it seems that it is the high frequency of parasitism rather than the virulence of parasitic young that has selected for anti-parasitic defences at the egg-stage, such as host-rejection behaviour of entire parasitised clutches (Fraga 1998; De Mársico *et al.* 2013). Clutch-rejection behaviour effectively limits the number of parasitic nestlings reared per nest, and thus the costs of competition to their own young (Fraga 1998; De Mársico *et al.* 2013). Nevertheless, the fact that Baywings have evolved discrimination against fledglings that do not resemble their own suggests that the fitness costs of rearing parasitic young to independence may be high enough to select for host defences at later stages of the nesting cycle (Fraga 1998; De Mársico *et al.* 2012). This might occur if competition with parasitic fledglings reduces the chances of host young surviving to adulthood (Rasmussen and Sealy 2006) or if increased post-fledgling parental care negatively affects the survival or future reproductive success of host parents (Payne and Payne 1998; Hoover and Reetz 2006). Further studies aimed to assess the costs of parasitism during and after the post-fledgling period would greatly contribute to the understanding of coevolutionary interactions between the Screaming Cowbird and its primary host. Our results suggest that, although the early lines of defence by Baywings do not eliminate the costs of parasitism entirely, host clutch-rejection behaviour combined with flexible nest-provisioning by cooperatively breeding groups may allow Baywing hosts to reduce their fitness losses under extremely high rates of brood parasitism.

Acknowledgements

We thank Fundación Elsa Shaw for allowing us to conduct the study at Reserva El Destino, and C. A. Ursino, M. G. Gantchoff and M. Chomnalez for field assistance during this study. M. C. De Mársico and J. C. Reboreda are research fellows of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). The study was supported by research grants of Agencia Nacional de Promoción Científica y Tecnológica (PICT-Raíces 2011-0045) and Universidad de Buenos Aires (UBACyT W808). Aves Argentinas-Asociación Ornitológica del Plata provided the aluminium leg bands used in this study. The study was conducted with the permission of the Provincial Organism for Sustainable Development (OPDS, Buenos Aires, Argentina) and complies with current laws of Argentina.

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