Animal Behaviour 86 (2013) 1023–1029

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

The wages of violence: mobbing by mockingbirds as a frontline defence against brood-parasitic cowbirds

Ros Gloag [a, *], Vanina D. Fiorini [b], Juan C. Reboreda [b], Alex Kacelnik [a]

[a] Department of Zoology, University of Oxford, Oxford, U.K.
[b] Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

ARTICLE INFO

Article history:
Received 2 June 2013
Initial acceptance 16 July 2013
Final acceptance 20 August 2013
Available online 1 October 2013
MS. number: 13-00471

Keywords:
brood parasitism
chalk-browed mockingbird
egg puncture
frontline defence
host–parasite coevolution
Mimus saturninus
Molothrus bonariensis
nest defence
shiny cowbird

For many hosts of brood-parasitic birds, their frontline of defence is to mob adult parasites that approach the nest. Mobbing is commonly interpreted as an adaptation to prevent the parasite from laying, although to date evidence of this is indirect or anecdotal. We investigated the effectiveness of mobbing by chalk-browed mockingbirds, *Mimus saturninus*, as a defence against their parasite, the shiny cowbird, *Molothrus bonariensis*, using videos of 480 naturally occurring cowbird nest visits and other direct observations. Mockingbirds only occasionally prevented cowbirds from reaching the nest or from laying once in it. More often, cowbirds were able to deposit an egg, aided by their agile flight, rapid laying, endurance of mobbing and, in some cases, opportunistic timing, whereby they approached nests when mockingbirds were distracted in battle with other cowbirds. Adult parasites present a second threat to hosts, however, in that they try to damage or remove host eggs prior to laying their own. We found that mobbing at the nest significantly reduced the likelihood that cowbirds broke a mockingbird egg during their visit, despite almost all mobbed visits concluding with a cowbird laying an egg. In this host therefore, the benefit of mobbing must be assessed by two independent measures: prevention of egg laying by the parasite and loss of their own eggs. As mockingbird eggs that survive a cowbird's visit intact can go on to fledge from parasitized broods, we expect strong selection for mobbing as an antiparasite defence in this host, even though it largely fails to prevent parasitism itself.

Brood-parasitic birds transfer the burden of parental care to their hosts by dumping their eggs in host nests, and hosts in response have evolved a variety of means to defend themselves against parasitism. Some host defences are enacted after parasitism, such as the detection and removal of foreign eggs or chicks from the nest (Rothstein 1975; Sato et al. 2010), or the rejection or abandonment of parasitized clutches (Langmore et al. 2003; Guigueno & Sealy 2011; De Mársico et al. 2013). Others are 'frontline' defences that precede or co-occur with the act of parasitism itself (Feeney et al. 2012).

Among the best-documented of hosts' frontline defences is the capacity to recognize adult parasites as a special threat and respond to them aggressively (Robertson & Norman 1976; Payne et al. 1985; McLean 1987; Briskie & Sealy 1989; Moksnes et al. 1991; Briskie et al. 1992; Mark & Stutchbury 1994; Webster 1994; Soler et al. 1999; Welbergen & Davies 2008; Fiorini et al. 2009a; Langmore et al. 2012; Trnka & Prokop 2012). We use the term mobbing to describe collectively these aggressive responses by hosts, which can include chasing, striking with the beak and feet, biting, swooping or knocking a parasite from air to ground. As for other frontline defences, mobbing is assumed to benefit hosts because it can prevent the parasite from laying its egg (Sealy et al. 1998; Feeney et al. 2012). Parasites should be deterred from entering a given nest if they have alternative opportunities where the expected risk of injury is lower. They may also choose to abort laying attempts if they are mobbed, because hosts that interact with parasites near their nest are more likely to reject the parasitic egg or young later (Davies & Brooke 1988; Moksnes et al. 1993; Bartol et al. 2002; Langmore et al. 2009; Guigueno & Sealy 2011). Compelling reports in a number of different systems tell of hosts successfully fending off parasites from their nests (Neudorf & Sealy 1994; Webster 1994; Budnik et al. 2001; Ellison & Sealy 2007; Kruger 2011) and even occasionally killing them (Molnár 1944; Moyer 1980). Welbergen & Davies (2009) also found indirect support that mobbing by reed warblers, *Acrocephalus scirpaceus*, reduces parasitism by common cuckoos, *Cuculus canorus*, by showing that those warbler pairs that mobbed a cuckoo mount suffered less parasitism than pairs that did not mob.

For some hosts, however, prevention of parasitism may not be the only or even the principal benefit accrued through mobbing

* Correspondence: R. Gloag, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.
E-mail address: ros.gloag@zoo.ox.ac.uk (R. Gloag).

0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2013.09.007

(Uyehara & Nairns 1995). In addition to adding their own egg to the host clutch, adult parasites typically present a second threat to host parents' fitness via the destruction or removal of host eggs. The cost to hosts of such egg loss varies between host–parasite pairs, but in some cases is high (Peer 2006). Indeed, where host young can be readily fledged alongside parasites, clutch reduction by female parasites can be the primary source of host offspring loss in parasitized nests (Massoni & Reboreda 2002; Peer 2006). Even for hosts whose offspring perish in the company of nestling parasites, egg loss will be worth minimizing provided they have some chance to remove the parasite in a subsequent line of defence (Rothstein 1975; Sato et al. 2010). Importantly, aggressive responses shown by hosts towards parasites need not affect the incidences of clutch reduction and parasitism equally. Tewksbury et al. (2002) found that this applied in the context of general nest attentiveness by yellow warblers, *Setophaga petechia*, at risk of parasitism by brown-headed cowbirds, *Molothrus ater*. Warblers that spent more time atop the nest were less likely to have an egg removed by cowbirds, but no less likely to be parasitized. If such a distinction also held for mobbing, then selection might sometimes favour this frontline defence primarily because it prevents parasites from destroying host eggs, rather than because it prevents parasitism per se.

In this study, we investigated mobbing by the chalk-browed mockingbird, *Mimus saturninus*, as a defence against their parasite, the shiny cowbird, *Molothrus bonariensis*. Female shiny cowbirds use their beaks to stab holes in eggs in host clutches, both when visiting the nest to lay and on separate nonlaying visits on preceding days (Ortega 1998). Hosts then remove these punctured eggs from the nest. Mockingbird nests are often parasitized by multiple cowbirds, with the result that previously laid cowbird eggs help to buffer mockingbird eggs against the puncture attacks of subsequent cowbirds (Gloag et al. 2012a). However, even with this clutch dilution benefit, egg loss from punctures remains a major source of fitness loss for parasitized mockingbirds (Fiorini 2007; Fiorini et al. 2009b). Mockingbird and cowbird eggs that survive unpunctured and hatch are reared together in mixed broods. Mockingbird parents incur the energetic costs of rearing parasitic young, but mockingbird chicks compete well against their cowbird nestmates and fledge from parasitized nests (Fiorini et al. 2009b; Gloag et al. 2012b).

Chalk-browed mockingbirds are almost twice the size of female cowbirds (70–75 g versus 40–45 g, respectively) and their interactions at the nest are among the most violent yet documented between hosts and adult parasites (Gloag et al. 2012a; see also Supplementary material, Videos 1–4). The consequences of mobbing for mockingbirds, however, remain unresolved. In a previous study, we reported that mockingbirds that attacked cowbirds at nests rarely stopped those cowbirds from laying or attacking eggs (Gloag et al. 2012a), but this estimate did not account for mobbing that occurred outside the nest, nor directly assessed the effect of mobbing on egg puncture success. Fiorini et al. (2009a) meanwhile reported that mockingbird pairs whose nests had not been parasitized were more aggressive towards model cowbirds than those whose nests had been parasitized, suggesting a role for mobbing in reducing parasitism risk. In this study, we used both recordings at the nest and observations outside the nest of naturally occurring interactions to determine the extent to which mobbing by mockingbirds succeeds in preventing both egg laying and egg breaking by shiny cowbirds, and whether these outcomes are independent of each other. In addition, we present data on the timing and behaviour of cowbirds during nest visits and discuss their potential counterdefences to host mobbing.

METHODS

Study Site and Species

We collected data at Reserva El Destino, Buenos Aires Province, Argentina (35°08′S, 57°23′W), during two breeding seasons, October–January 2010–2011 and 2011–2012. The site is pampas grassland, punctuated by small clumps of trees, predominantly tala, *Celtis tala*, coronillo, *Scutia buxifolia*, and molle, *Schinus longifolius*. We monitored the nesting attempts of approximately 40 chalk-browed mockingbird pairs per season. Each pair holds a territory centred upon one or more tree clumps, in which they build large open nests of sticks, lined with hair (Fraga 1985). Following an unsuccessful nesting attempt, pairs will construct a new nest in a new location within their territory (Fraga 1985). High rates of predation, and also abandonment after clutch reduction by cowbirds, mean that most pairs build several nests per season (median = 5, range 1–10, $N = 41$). We treated nests built in the same territory as having been built by the same pair. The incidence and intensity of cowbird parasitism on mockingbirds at this site are high: a recent study found 89% of nests were parasitized, 70% multiply (median = 3 eggs, range 1–12 eggs, Gloag et al. 2012a). Mockingbirds have no known defences at later stages in the breeding cycle, with the exception of rejecting one morph of cowbird egg laid uncommonly in their nests, the unspotted white morph (de la Colina et al. 2012).

Filming and Observation at Nests

Mockingbirds lay a clutch of four eggs and most parasitism occurs within the period of mockingbird laying (Fiorini & Reboreda 2006). During this interval, we fixed 'nest cams' into the vegetation above nests (Handykam CCD colour microcameras), attached to digital video recorders (Lawmate PVR1000 or PVR500 ECO) and power sources concealed on the ground. Nest cams were positioned as quickly as possible to minimize disturbance at nests and mockingbirds were seen to resume normal behaviour at nests shortly after camera placement. Nests were filmed each day during the mockingbird's laying period, or until the nest was predated or abandoned. We considered a nest to be abandoned if the mockingbirds did not appear at the nest during the day's recording. This criterion was supported by the fact that mockingbirds began new nesting attempts several days to 1 week later in all cases. We filmed a total of 597 days at 213 nests (2010–2011: 88 nests, 41 pairs; 2011–2012: 125 nests, 38 pairs). When possible we filmed nests from 1 h prior to sunrise until sunset ($N = 271$ days), but where active nests were discovered after sunrise or equipment was limiting we recorded partial days (minimum 6 h, $N = 326$ days). Cowbirds generally visit nests both to puncture eggs and to lay in the period between civil twilight and sunrise, and thereafter visit nests to puncture eggs only (see Results). The contents of all filmed nests were checked each day in order to label new eggs, and record any eggs that had been broken but not removed by mockingbirds from the nest. Labels were made with a fine-tipped black marker and comprised a single digit indicating egg number. Cowbird eggs were also labelled with date and nest number.

Nest cams captured only events at the nest. To assess whether mockingbirds were able to prevent cowbirds from reaching the nest, observations were made at 28 active nests in which nest cams were deployed, each in a different breeding territory. Observation sessions were timed to coincide with cowbird egg laying, beginning 45 min prior to sunrise and concluding 15 min after sunrise, with nests receiving either a single session ($N = 21$ nests), or two sessions, one each day on consecutive days ($N = 7$ nests). The observer (R.G.) was concealed in the long grass 10–15 m from the tree

containing the nest, prior to first light, and noted whether a cowbird approached the tree containing the nest (i.e. was flying directly towards the tree when within a radius of 15 m or less from the tree), whether it was mobbed by mockingbirds (chased out of the observer's view, struck with the beak or feet or knocked to the ground), and whether it succeeded in entering the tree.

All work complied with Argentinean Law, and was undertaken with permission from Organismo Provincial de Desarrollo Sostenible, Argentina.

Mobbing Effectiveness

We examined two routes by which mockingbirds' mobbing could impede parasite laying: preventing the parasite from reaching the nest and from laying once there. All arrival times for cowbird nest visits were standardized relative to sunrise on the day of recording (civil twilight = 28 ± 1 min before sunrise in all cases, U.S. Naval Observatory data, http://www.usno.navy.mil/). For mobbing outside the nest, we report the success rate of mobbing with the assumption that all cowbirds that approached the nest prior to sunrise would lay an egg if undisturbed. This assumption leads to an upper estimate of mobbing's effectiveness because a small proportion of presunrise visits may be nonlaying visits (see Results). To compute the effectiveness of mobbing in preventing a cowbird laying once it is in the nest, we compared the incidence of egg laying among mobbed presunrise visits to that among visits in the same period that were not mobbed (Fisher's exact test). We excluded from our analysis two presunrise visits to active nests in which no laying occurred because prior to the cowbird's visit these nests were either predated ($N = 1$) or became filled with sticks (knocked into the nest by a chimango, *Milvago chimango*, $N = 1$), which probably caused the cowbird to abort its laying attempt. As we filmed multiple nesting attempts per mockingbird territory, and multiple days of each nesting attempt, some nests and individuals were represented more than once in the final data set. When appropriate, we report results from both our complete data set and for a subset of data that includes only the first recorded event per territory.

Independent of egg laying, mobbing could prevent cowbirds from breaking eggs in the nest in one or both of two ways. First, it could reduce the likelihood that a cowbird that has reached the nest will succeed in puncturing an egg, even if that cowbird then lays. We used a forward stepwise logistic regression to relate the occurrence of mobbing to the likelihood that cowbirds in the nest broke at least one mockingbird egg (dependent variable: egg broken/no egg broken). We considered nests that contained only mockingbird eggs at the time of a cowbird's visit and for which we were able to attribute a broken egg to a single nest visit. In addition to our predictor variable of interest (cowbird mobbed/not mobbed), we included number of eggs present (1–4), mockingbird territory ID and all pairwise interaction terms as predictor variables. Variables were entered into the model if the resulting reduction in deviance was larger than the critical value of chi-square at $\alpha = 0.05$ and $df = 1$. We then assessed the final model's fit based on the reduction in deviance of the model relative to the null model with intercept only (Δdev). We also performed a Fisher's exact test to compare directly the proportion of cowbird visits that resulted in mockingbird egg loss when mobbing did or did not occur. Finally, we used general linear models to compare the duration of puncture attacks (s) and the latency to lay an egg once in the nest (s) for cowbirds making presunrise visits when mobbed and when not mobbed. This allowed us to assess whether mobbing functions specifically by causing cowbirds to truncate their puncture attacks.

The second way in which mobbing could prevent egg loss is by preventing cowbirds from reaching the nest to make nonlaying visits. Nest cams captured interactions that occurred at the nest for such visits. In the case of mobbing outside the nest, the low incidence of nonlaying visits per hour (see Results) made direct focal observations impractical. Instead, we took advantage of nest cam recordings made at recently abandoned nests to make an indirect estimate of the effect of defence outside the nest in deterring nonlaying visits. We compared the proportion of active nests receiving a cowbird visit (or visits) during a day's recording to that of nests that had been abandoned less than 24 h previously (Fisher's exact test). We chose to compare visited/unvisited proportions rather than visit rate as a continuous variable, because the great majority of nests received either one or zero visits and the resulting distribution was strongly zero skewed (although hourly cowbird visit rates are also reported). If mobbing (or the threat of mobbing i.e. nest guarding) deterred cowbirds from making nonlaying visits we expected the proportion of active nests receiving visits to be less than that of nests recently abandoned. A possible confounding factor in this comparison is that the presence of the mockingbird pair could increase the detectability of the nest (Sealy et al. 1998), but this would be expected to generate bias in the opposite direction (i.e. active nests more likely to receive cowbird visits). Also, most cowbirds visiting nests during the host's laying period will be returning to nests they had discovered during the nest construction phase (Fraga 1985; Wiley 1988; Kattan 1997; Banks & Martin 2001).

Cowbird Behaviour

We assessed three aspects of the cowbird's behaviour that we considered to be relevant to the mockingbird's mobbing defence: the distribution of cowbird nest visits throughout the day, visit duration and the synchronicity of cowbirds' presunrise visits in cases of same-day multiple parasitism.

Visit schedule

We calculated the risk that a nest receives a cowbird visit per hour by computing the proportion of all nests filmed in a given hour that received at least one cowbird visit. Confidence intervals (95%) were calculated using the exact method (Zar 1999).

Visit duration

We calculated the time (s) cowbirds spent in the nest during a visit and, where egg laying occurred and our view of the cowbird was not obstructed, the time (s) taken to lay (measured as the interval between the cowbird ceasing a puncture attack and laying its egg, which is evidenced by the brief raising and inflating of the body). Shiny cowbirds do not continue puncture attacks during or after egg laying, presumably so as not to risk damaging their own egg.

Synchronicity of same-day parasitism

We noticed that when two or more cowbirds parasitized a nest on the same morning, the interval between their arrivals was often very short, such that mockingbirds were still engaged in mobbing the first cowbird, or inspecting their damaged clutch, when the second cowbird arrived. We reasoned that this could reflect an active behaviour by cowbirds. For example, cowbirds could show an opportunistic tendency to approach nests when mockingbirds were distracted. If so, then the proportion of same-day laying visits in which a female 'tailed' another female to the nest would be higher than that expected by chance. We tested this using a Monte Carlo simulation, in which x was the total number of filmed nests that received multiple presunrise cowbird visits on the same day, and y was the number of those nests for which the arrival interval between females was less than 60 s (where intervals this small

were deemed to be 'tailed' visits). For nests parasitized more than twice on the same morning, we considered only the intervals between the first two parasitic events. Drawing random samples from the pool of observed arrival times relative to sunrise on the day of recording, across all filmed laying visits, we generated a frequency distribution of expected tailed visits if cowbird arrival times were independent, based on 100 000 simulations drawing with replacement. We considered the observed number of cowbirds tailing other cowbirds to the nest to be significantly higher than chance if it fell above the 95th percentile of this distribution. We also tested whether the probability of being mobbed at the nest differed between cowbirds that tailed and those cowbirds that preceded them, using McNemar's test (Zar 1999).

We used MatLab (Mathworks, Natick, MA, U.S.A.) and SPSS v20.0 (SPSS Inc., Chicago, IL, U.S.A.) for statistical tests in this study. Errors reported are SEMs.

RESULTS

Does Mobbing Prevent Parasites Laying Eggs?

The majority of nest visits in which the cowbird laid an egg occurred prior to sunrise (238/257, 92%), with the remainder occurring in the 30 min after sunrise (mean time of laying ± SE: 14 ± 1 min before sunrise). The probability of mockingbirds receiving one or more cowbird visits during the presunrise hour was high, with just over half of nests visited (Fig. 1). Mobbing was also common during this period, occurring on 213 of 259 presunrise visits (82%, e.g. Supplementary material Video 1). This proportion was similar when we considered only the first cowbird nest visit in each mockingbird territory (29/37, 78%).

From the moment puncture attacks ceased, cowbirds took on average ± SE 6.3 ± 0.9 s to lay an egg (range 2.1–16.2 s, $N = 153$), but their total time in the nest was typically longer owing to the time spent attempting to puncture eggs and being detained after laying by the mobbing of mockingbirds (mean ± SE: 19.7 ± 1.6 s, range 4–130 s, $N = 259$). During mobbing, mockingbirds delivered on average ± SE 17 ± 2.0 blows with the beak to the head and body of the cowbird while it was in the nest (range 0–127, $N = 259$). Mobbing events were often noisy, with both mockingbirds and cowbirds making calls during the attack (e.g. Supplementary material Videos 2, 3). At one nest (which we did not film) we found a dead female cowbird, with an egg low in her oviduct, impaled belly-up on a *coronillo* thorn just 30 cm below a nest. This death presumably resulted from being pushed onto the thorn by the weight of attacking mockingbirds (a fatal version of the type of scenario seen in Supplementary material Video 4). Such extreme outcomes, however, are probably rare, and in all nest cam recordings mobbed cowbirds were seen to fly away from the nest without apparent injuries. Furthermore, mobbing at the nest generally failed to prevent cowbirds laying. In only 17 of the 213 mobbed visits we filmed did the cowbird flee the nest without adding an egg, and nine of these were followed the same morning by a successful laying visit, which could have been the female returning or another cowbird. The proportion of mobbed visits that did not result in egg laying was therefore at most 8% and was not significantly greater than the incidence of egg laying by cowbirds that made presunrise nest visits but were not mobbed (3/46; Fisher's exact test: $P = 0.19$; Fig. 2).

Direct observations made before sunrise revealed that mobbing also occurs outside the nest. At all observed nests ($N = 28$), mockingbird parents assumed conspicuous perches from first twilight on high branches close to the nest (<5 m). We witnessed a total of 27 attempts by cowbirds to approach 17 nests, of which 26 featured mobbing. Cowbirds shot rapidly towards nests from concealed positions in the long grass or nearby vegetation, prompting one or both mockingbirds to leave their perch and try to intercept the

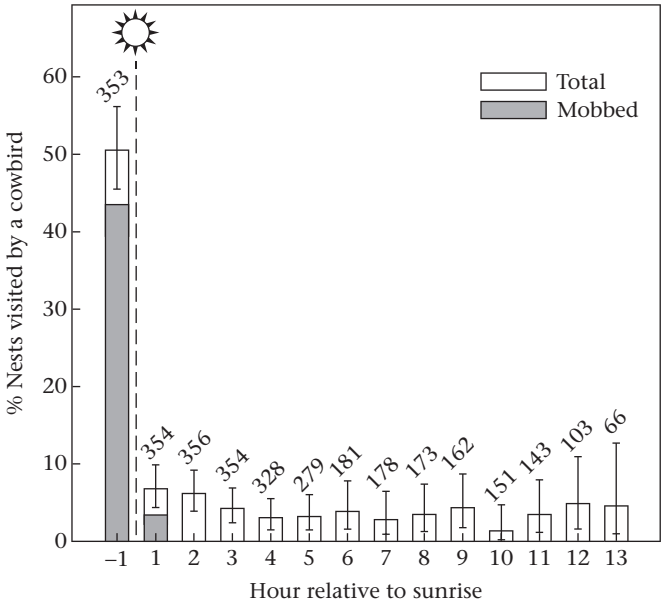

Figure 1. The percentage of active chalk-browed mockingbird nests filmed in a given hour relative to sunrise that received at least one visit from a cowbird, with 95% confidence intervals. Grey shading on bars indicates the percentage of nests filmed in a given hour for which the owners mobbed at least one cowbird at the nest. Nests were filmed during the 4 days of the mockingbird's laying period, when most parasitism occurs. Cowbird visits before or just after sunrise usually involved both egg puncturing and egg laying, while those that occurred subsequently involved egg puncturing only. Sample sizes for the number of recordings used to calculate each hour's percentages are given above each bar. Note that this figure plots the risk of a nest receiving at least one cowbird visit, and that some nests will receive two or more visits in the same hour.

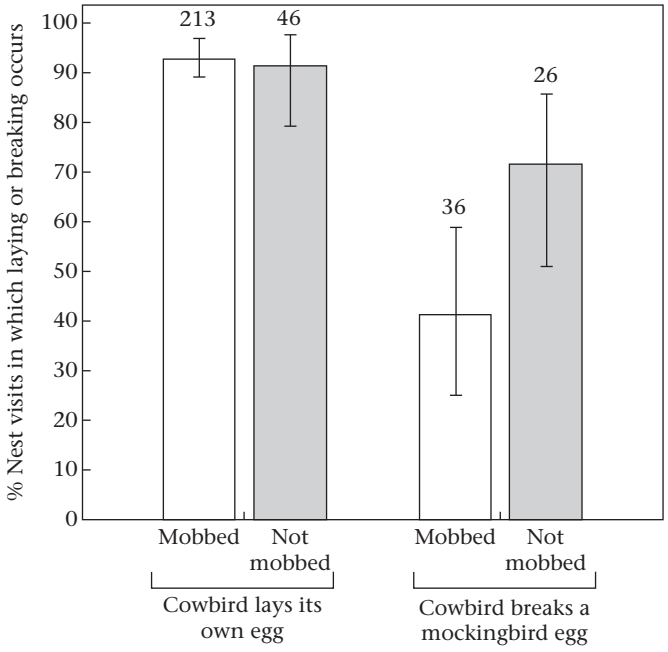

Figure 2. The percentage of visits made by shiny cowbirds to nests of chalk-browed mockingbirds in which the cowbird succeeded in laying an egg or breaking at least one mockingbird's egg when they were mobbed in the nest by mockingbirds (white bars) or not mobbed (grey bars), with 95% confidence intervals. Egg-laying success was assessed based only on visits that occurred prior to sunrise. Sample sizes are given above the bars.

cowbird mid-air. This led to aerial dogfights, with mockingbirds pursuing cowbirds as they twisted and turned attempting to reach the tree. Mobbing outside the nest thus consisted mostly of chasing, although one cowbird was grabbed mid-air and pulled briefly to the ground, before taking to the air again. In 22 cases, the cowbird outmanoeuvred the mockingbird and entered the tree with the mockingbird in tow (81%; nest cams indicated that these cowbirds were then mobbed in the nest). In the remaining four cases, the cowbird instead fled into nearby vegetation. Two of these four attempts that morning were followed, however, by successful egg laying by a cowbird, which may have been the same female returning. Based on these observations, mobbing outside the nest thus succeeded in preventing at most 15% of parasitism (4/26 attempts) and at least 8% (2/24 attempts, if two were the same female returning). This estimate was similar if we considered only the first observed interaction in each mockingbird territory (2/17 attempts, 12%). These may be upper estimates of mobbing's effectiveness outside the nest, given that nest cams showed that a small proportion of cowbirds making presunrise visits did not lay an egg despite not being mobbed (3/46, 6.5%).

The single cowbird that we observed reaching the nest unchallenged made its approach moments after both mockingbirds had rushed to the nest in pursuit of a previous cowbird. Nest cam recordings revealed that tailing other females in this way was not rare. We filmed 52 cases of same-day parasitism, of which 16 showed the second cowbird arriving at the nest within 60 s of the previous cowbird (31%, e.g. Supplementary material Videos 2, 3, 4). A Monte Carlo simulation showed that this was significantly more than expected by chance if the arrival times of cowbirds were independent (Fig. 3), consistent with tailing being an active cowbird behaviour. Tailing could result in cowbirds eluding mobbing outside the nest, but once at the nest second-to-arrive cowbirds were no less likely to be mobbed than the cowbird that preceded them (11/16 mobbed and 14/16 mobbed, respectively; McNemar's test: $\chi^2_1 = 1.3$, $P = 0.25$). On four occasions, tailing resulted in two cowbirds occupying the nest at the same time (e.g. Supplementary material Video 3), in which case they jostled for space in the nest but did not otherwise interfere with each other's laying.

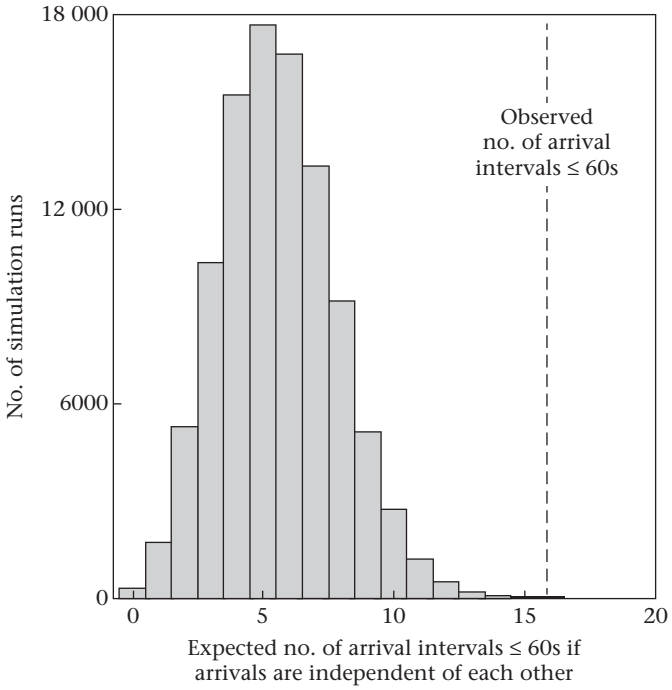

Figure 3. The number of arrival intervals ≤60 s that we observed in our sample of 52 cases of same-day multiple parasitism ($N = 16$, dashed line) and the frequency distribution of expected observations of cowbird arrivals at ≤60 s intervals in 52 pairs of visits if cowbirds arrive independently of each other (i.e. if arrival intervals ≤60 s are generated by chance alone). The observed number falls above the distribution's 95th percentile, indicating that such visits occurred significantly more frequently than expected by chance. The frequency distribution was generated from a Monte Carlo simulation with 100 000 runs, drawing pairs of arrival times (relative to sunrise) randomly from a pool of all recorded arrival times on which an egg was laid (see Methods, $N = 288$).

Does Mobbing Prevent Parasites from Breaking Eggs?

We were able to determine the fate of mockingbird eggs following 62 filmed cowbird visits to nests that contained only mockingbird eggs. The proportion of visits that resulted in broken eggs was lower when cowbirds were mobbed at the nest than when they were not (Fig. 2; mobbed: 15/36 visits; not mobbed: 20/26 visits; Fisher's exact test: $P = 0.009$). A logistic regression indicated that mobbing was significantly associated with the odds of egg loss (mean coefficient of constant ± SE = 1.2 ± 0.47, mean coefficient of mobbing ± SE = −1.54 ± 0.58; Δdev = 7.9, $df = 1$, $P = 0.005$) while clutch size, territory ID and interaction terms did not significantly improve the fit of the model (although clutch size did closely approach the threshold for inclusion: $P = 0.09$). In most mobbed visits in which egg loss was prevented, the cowbird nevertheless laid her own egg (19/21, 90%). Mobbed cowbirds spent less time in the nest prior to laying and less time puncturing eggs than those that were not mobbed (latency to lay: mobbed ± SE = 11.3 ± 0.6 s, $N = 128$, not mobbed ± SE = 16 ± 1.9 s, $N = 70$; $F_1 = 8.8$, $P = 0.004$; puncture attack duration: mobbed ± SE = 2.7 ± 0.2 s, $N = 169$, not mobbed ± SE = 7.8 ± 1.7 s, $N = 70$; $F_1 = 21.2$, $P < 0.001$).

The cumulative risk of receiving at least one postsunrise visit was similar to that for presunrise visits, but as this was divided roughly evenly across all postsunrise daylight hours, the risk of a visit per hour was much lower after sunrise (Fig. 1). Nest cams revealed that once at the nest, cowbirds making postsunrise visits were mobbed infrequently (23/161, 14%), and rarely for visits occurring more than 1 h after sunrise (5/130, 4%, e.g. Supplementary material Video 5). A comparison of postsunrise visits at active and abandoned nests, however, suggested that mockingbird defence occurring outside a nest cam's field-of-view did deter cowbirds from making visits. Nests that had been abandoned within the 24 h preceding filming were significantly more likely to attract postsunrise visits than active nests (Fisher's exact test: $P < 0.001$; 23/46 abandoned nests, but only 95/383 active nests, received at least one cowbird visit; mean visit rate for abandoned nests ± SE = 0.12 ± 0.02 per hour, mean visit rate for active nests ± SE = 0.05 ± 0.005 per hour). Most postsunrise visits involved a lone female cowbird (97%, 130/134) although occasionally a second female was also present (3%, 4/134).

In 236 filmed nest visits in which cowbirds were mobbed, we only once observed a mockingbird puncture its own egg while striking at a cowbird, indicating that the risk of such accidents is low.

DISCUSSION

Mobbing as a Defence Against Egg Puncture

The most conspicuous defence employed by chalk-browed mockingbirds against their brood parasite, the shiny cowbird, is the vigorous mobbing of adult cowbirds near the nest during the early nesting stages. At first glance this defence does not seem particularly effective. Direct observations of hundreds of naturally occurring interactions revealed that mobbing only occasionally

prevented cowbirds from reaching the nest, and that once cowbirds were in the nest, mobbing did not reduce the likelihood that they laid eggs. However, by mobbing, mockingbirds were able to reduce the chance that their eggs were broken during a cowbird's puncture attack. It is likely that it is this second measure of mobbing's success that confers the greatest benefit on mockingbirds, as higher egg survivorship will result in a greater number of mockingbird offspring reared in parasitized broods. Mobbing by mockingbirds thus illustrates that hosts' frontline defences against brood parasites might be strongly favoured by selection even where they have little effect on the incidence of parasitism itself.

The risk of a cowbird visit varied greatly throughout the day, being high in the hour before sunrise, when 50% of mockingbird nests received at least one visit, and then falling to one-tenth or less of this risk for each hour thereafter. Mockingbirds mobbed the majority of cowbirds that entered the nest before sunrise, but few of those that entered after sunrise. There are two possible explanations for this temporal variation in the incidence of mobbing at the nest. First, mockingbirds may attend more closely to their nests during the presunrise period, either in response to the peak in parasitism risk in this hour (Neudorf & Sealy 1994) or because it is adaptive to stick close to the nest before sunrise for reasons unrelated to parasitism (Kacelnik & Krebs 1982). Second, postsunrise nest defence may consist simply of nest guarding, rather than mobbing inside the nest. This assumes that, unlike presunrise visits when cowbirds are physiologically committed to egg laying, females making nonlaying visits will approach a nest only if it is unguarded. We found that the incidence of postsunrise visits made to newly abandoned nests (i.e. where mockingbirds were no longer attentive), was higher than that to active nests, consistent with nest guarding (and the threat of mobbing it represents) reducing the number of cowbirds' postsunrise puncture attacks.

Yellow warblers, a host of the brown-headed cowbird, will respond to female cowbirds by sitting tight on the nest and shielding their clutch with their bodies (Burgham & Picman 1989; Hobson & Sealy 1989; Gill & Sealy 1996). This may not prevent parasitism, as cowbirds will lay on or beside hosts, leaving their eggs to roll into the nest when hosts move (Neudorf & Sealy 1994; Ellison & Sealy 2007) although tight sitting presumably does function well to prevent egg loss or puncture. The trade-offs that determine whether mobbing or tight sitting is favoured in a given host remain unclear. One recorded instance of a shiny cowbird arriving at a mockingbird nest when the female was incubating shows the cowbird successfully displacing her and puncturing eggs (Gloag et al. 2012a), so perhaps shiny cowbirds are simply too tenacious for clutches to be protected in this way, even by large hosts. Our results also show that mockingbird mobbing leads to a modest reduction in the number of cowbirds reaching the nest, with these cowbirds thus prevented from both egg puncturing and laying. Finally, mobbing might have benefits over tight sitting that were not revealed in the present study. For example, cowbirds might learn to avoid parasitizing mockingbird territories where they have been most severely beaten in the past. Each female cowbird lays just one egg per mockingbird nest, but they do maintain a constant home range and can parasitize successive breeding attempts in a given mockingbird territory (R. Gloag, unpublished data). Such a deterrent effect would be consistent with the findings of Fiorini et al. (2009a), whereby pairs more aggressive towards model cowbirds suffered lower parasitism rates. It would also indicate a benefit to mockingbirds of continuing to mob cowbirds at the nest that have already laid and are trying to escape, which we sometimes observed to occur (e.g. Supplementary material Video 4).

Selection pressures on different lines of host defences are likely to be interdependent (Soler et al. 1999; Røskaft et al. 2002; Britton et al. 2007; Kilner & Langmore 2011) and may even be antagonistic. Thus a host that can reliably detect and reject foreign eggs from the nest may experience relaxed selection for the ability to do likewise with foreign nestlings (Kilner & Langmore 2011). It is worth noting that frontline defences that reduce host egg loss independently of reducing parasitism could also influence the evolution of later lines of defence. For example, greater own egg survival may facilitate the evolution of parasite recognition and rejection by discordancy (i.e. the rejection of parasite eggs or chicks using an 'odd-one-out' rule; Moskát et al. 2009) by ensuring that parasite eggs are reliably outnumbered by host eggs.

Counterdefences to Mobbing in Shiny Cowbirds?

Any successful host defence may provoke counterdefences in parasites. Just as for mockingbirds, the outcome of frontline battles for cowbirds can be measured on two scales: one for egg puncture and the other for egg laying. Getting the egg into the nest is paramount, while successful egg puncture will increase the likelihood that the resulting offspring survives to fledge (Fiorini et al. 2009b; Gloag et al. 2012b). Shiny cowbirds have a number of traits that aid them in their frontline battle with mockingbirds, although whether these have evolved as counterdefences to host aggression specifically or as adaptations to parasitism more generally is not easily assessed. Agile, rapid flight helps female cowbirds to outmanoeuvre mockingbirds on the wing in order to reach the nest. Once in the nest, mean laying time was just under 7 s, and mean time spent in the nest including egg puncturing (itself extremely rapid) around 20 s. These estimates are similar to those from other brood-parasitic birds, and far lower than those of nonparasites for which laying bout duration typically averages 20 min or more (Sealy et al. 1995). Furthermore, shiny cowbirds are able to puncture eggs and lay while enduring a forceful barrage of blows to the head, eyes and body from a host (or two) almost twice their size. Merrill et al. (2012) found that following a period of acute stress, male brown-headed cowbirds suffered immune suppression but females did not, leading the authors to propose that the physiology of females' stress responses are adapted for a parasitic lifestyle. It would be interesting to investigate whether the impressive endurance of female shiny cowbirds to mobbing is associated with adaptations in stress tolerance.

Finally, we found that around one-third of all the same-day multiple parasitism we filmed involved a second female closely tailing a preceding female to the nest (the two arriving less than 60 s apart), and that this incidence was too high to be explained by chance. On arriving at the nest, cowbirds that had tailed a conspecific were no less likely to be mobbed than the cowbird that preceded them. However, because mockingbirds will still be at or near the nest when the second cowbird arrives, tailing presumably does increase the likelihood that a cowbird bypasses the initial prenest phase of mobbing. Tailing may thus represent opportunism on behalf of cowbirds as a strategy to evade being mobbed when approaching the nest. If so, cowbird arrivals should tend to coincide with any event that distracts mockingbirds away from their guard perches. An alternative, intriguing explanation for tailing is that it represents eavesdropping on the part of the second-to-arrive females, which do not know the location of a suitable nest and so have followed a conspecific from a communal night roost. We found that very few presunrise nest visits by cowbirds did not involve laying, indicating that females select the nest they will parasitize during the preceding day or days, rather than prospect among known nests on the morning of laying. Even so, a female could find itself unexpectedly without a suitable nest because of nest predation, or lack the necessary experience to locate nests readily (e.g. young females). If tailing is the result of eavesdropping

then any evasion of mobbing that it affords is a secondary advantage. The gregarious habits of female shiny cowbirds have been noted anecdotally on several occasions (Fraga 1985; Wiley 1988; Kattan 1997), but the possibility that these parasites use social learning to locate host nests in this or other contexts requires further investigation.

Acknowledgments

We thank Juan Shaw and the Elsa Shaw de Pearson Foundation for supporting our fieldwork at Reserva El Destino. We are grateful to Agencia Nacional de Promoción Científica y Tecnológica (Proyecto PICT Raíces 2006-00215) and The Cogito Foundation for funding. R.G. was supported by a University of Oxford Clarendon Fund postgraduate scholarship. J.C.R. and V.D.F. are Research Fellows of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2013.09.007.

References

Banks, A. J. & Martin, T. E. 2001. Host activity and the risk of nest parasitism by brown-headed cowbirds. *Behavioral Ecology*, **12**, 31–40.

Bartol, I., Karcza, Z., Moskát, C., Røskaft, E. & Kisbenedek, T. 2002. Responses of great reed warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. *Journal of Avian Biology*, **33**, 420–425.

Briskie, J. V. & Sealy, S. G. 1989. Changes in nest defense against a brood parasite over the breeding cycle. *Ethology*, **82**, 61–67.

Briskie, J. V., Sealy, S. G. & Hobson, K. A. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. *Evolution*, **46**, 334–340.

Britton, N. F., Planque, R. & Franks, N. R. 2007. Evolution of defence portfolios in exploiter-victim systems. *Bulletin of Mathematical Biology*, **69**, 957–988.

Budnik, J. M., Burhans, D. E., Ryan, M. R. & Thompson, F. R. 2001. Nest desertion and apparent nest protection behavior by Bell's vireos in response to cowbird parasitism. *Condor*, **103**, 639–643.

Burgham, M. C. J. & Picman, J. 1989. Effect of brown-headed cowbirds on the evolution of yellow warbler anti-parasite strategies. *Animal Behaviour*, **38**, 298–308.

de la Colina, M. A., Pompilio, L., Hauber, M. E., Reboreda, J. C. & Mahler, B. 2012. Different recognition cues reveal the decision rules used for egg rejection by hosts of a variably mimetic avian brood parasite. *Animal Cognition*, **15**, 881–889.

Davies, N. B. & Brooke, M. D. L. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour*, **36**, 262–284.

De Mársico, M. C., Gloag, R., Ursino, C. A. & Reboreda, J. C. 2013. A novel method of rejection of brood parasitic eggs reduces parasitism intensity in a cowbird host. *Biology Letters*, **9**, 20130076.

Ellison, K. & Sealy, S. G. 2007. Small hosts infrequently disrupt laying by brown-headed cowbirds and bronzed cowbirds. *Journal of Field Ornithology*, **78**, 379–389.

Feeney, W. E., Welbergen, J. A. & Langmore, N. E. 2012. The frontline of avian brood parasite-host coevolution. *Animal Behaviour*, **84**, 3–12.

Fiorini, V. D. 2007. *Sincronización de puesta y elección de hospedador en el parásito de cría generalista* Molothrus bonariensis *(Icterinae, Aves)*. Ph.D. thesis. University of Buenos Aires.

Fiorini, V. D. & Reboreda, J. C. 2006. Cues used by shiny cowbirds (*Molothrus bonariensis*) to locate and parasitise chalk-browed mockingbird (*Mimus saturninus*) nests. *Behavioral Ecology and Sociobiology*, **60**, 379–385.

Fiorini, V. D., Tuero, D. T. & Reboreda, J. C. 2009a. Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by shiny cowbirds in chalk-browed mockingbirds. *Behaviour*, **146**, 1387–1403.

Fiorini, V. D., Tuero, D. T. & Reboreda, J. C. 2009b. Shiny cowbirds synchronize parasitism with host laying and puncture host eggs according to host characteristics. *Animal Behaviour*, **77**, 561–568.

Fraga, R. M. 1985. Host–parasite interactions between chalk-browed mockingbirds and shiny cowbirds. *Ornithological Monographs*, **36**, 829–844.

Gill, S. A. & Sealy, S. G. 1996. Nest defence by yellow warblers: recognition of a brood parasite and an avian nest predator. *Behaviour*, **133**, 263–282.

Gloag, R., Fiorini, V. D., Reboreda, J. C. & Kacelnik, A. 2012a. Brood parasite eggs enhance egg survivorship in a multiply parasitized host. *Proceedings of the Royal Society B*, **279**, 1831–1839.

Gloag, R., Tuero, D. T., Fiorini, V. D., Reboreda, J. C. & Kacelnik, A. 2012b. The economics of nestmate-killing in avian brood parasites: a provisions trade-off. *Behavioral Ecology*, **23**, 132–140.

Guigueno, M. F. & Sealy, S. G. 2011. Aggression towards egg-removing cowbird elicits clutch abandonment in parasitized yellow warblers, *Dendroica petechia*. *Animal Behaviour*, **81**, 211–218.

Hobson, K. A. & Sealy, S. G. 1989. Responses of yellow warblers to the threat of cowbird parasitism. *Animal Behaviour*, **38**, 510–519.

Kacelnik, A. & Krebs, J. R. 1982. The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour*, **83**, 287–309.

Kattan, G. H. 1997. Shiny cowbirds follow the 'shotgun' strategy of brood parasitism. *Animal Behaviour*, **53**, 647–654.

Kilner, R. M. & Langmore, N. E. 2011. Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. *Biological Reviews of the Cambridge Philosophical Society*, **86**, 836–852.

Kruger, O. 2011. Brood parasitism selects for no defence in a cuckoo host. *Proceedings of the Royal Society B*, **278**, 2777–2783.

Langmore, N. E., Hunt, S. & Kilner, R. M. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature*, **422**, 157–160.

Langmore, N. E., Cockburn, A., Russell, A. F. & Kilner, R. M. 2009. Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behavioral Ecology*, **20**, 978–984.

Langmore, N. E., Feeney, W. E., Crowe-Riddell, J., Luan, H., Louwrens, K. M. & Cockburn, A. 2012. Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*. *Behavioral Ecology*, **23**, 798–805.

McLean, I. G. 1987. Response to a dangerous enemy: should a brood parasite be mobbed? *Ethology*, **75**, 235–245.

Mark, D. & Stutchbury, B. J. 1994. Response of a forest-interior songbird to the threat of cowbird parasitism. *Animal Behaviour*, **47**, 275–280.

Massoni, V. & Reboreda, J. C. 2002. A neglected cost of brood parasitism: egg punctures by shiny cowbirds during inspection of potential host nests. *Condor*, **104**, 407–412.

Merrill, L., Angelier, F., O'Loghlen, A. L., Rothstein, S. I. & Wingfield, J. C. 2012. Sex-specific variation in brown-headed cowbird immunity following acute stress: a mechanistic approach. *Oecologia*, **170**, 25–38.

Moskát, C., Hauber, M. E., Aviles, J. M., Ban, M., Hargitai, R. & Honza, M. 2009. Increased host tolerance of multiple cuckoo eggs leads to higher fledging success of the brood parasite. *Animal Behaviour*, **77**, 1281–1290.

Moksnes, A., Røskaft, E., Braa, A. T., Korsnes, L., Lampe, H. M. & Pedersen, H. C. 1991. Behavioral responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour*, **116**, 64–89.

Moksnes, A., Røskaft, E. & Korsnes, L. 1993. Rejection of cuckoo (*Cuculus canorus*) eggs by meadow pipits (*Anthus pratensis*). *Behavioral Ecology*, **4**, 120–127.

Molnár, B. 1944. The cuckoo in the Hungarian plain. *Aquila*, **51**, 100–112.

Moyer, D. C. 1980. On lesser honeyguide and black-collared barbet. *Zambian Ornithological Society Newsletter*, **10**, 159.

Neudorf, D. L. & Sealy, S. G. 1994. Sunrise nest attentiveness in cowbird hosts. *Condor*, **96**, 162–169.

Ortega, C. P. 1998. *Cowbirds and Other Parasites*. Tucson: The University of Arizona Press.

Payne, R. B., Payne, L. L. & Rowley, I. 1985. Splendid wren *Malurus splendens* response to cuckoos: an experimental test of social organization in a communal bird. *Behaviour*, **94**, 108–126.

Peer, B. D. 2006. Egg destruction and egg removal by avian brood parasites: adaptiveness and consequences. *Auk*, **123**, 16–22.

Robertson, R. J. & Norman, R. F. 1976. Behavioral defenses to brood parasitism by potential hosts of the brown-headed cowbird. *Condor*, **78**, 166–173.

Røskaft, E., Moksnes, A., Stokke, B. G., Bicik, V. & Moskát, C. 2002. Aggression to dummy cuckoos by potential European cuckoo hosts. *Behaviour*, **139**, 613–628.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor*, **77**, 250–271.

Sato, T., Tokue, K., Noske, R. A., Mikami, O. K. & Ueda, K. 2010. Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. *Biology Letters*, **6**, 67–69.

Sealy, S. G., Neudorf, D. L. & Hill, D. P. 1995. Rapid laying by brown-headed cowbirds *Molothrus ater* and other parasitic birds. *Ibis*, **137**, 76–84.

Sealy, S. G., Neudorf, D. L., Hobson, K. A. & Gill, S. A. 1998. Nest defense by potential hosts of the brown-headed cowbird: methodological approaches, benefits of defence, and coevolution. In: *Parasitic Birds and their Hosts: Studies in Coevolution* (Ed. by S. I. Rothstein & S. K. Robinson), pp. 194–211. New York: Oxford University Press.

Soler, J. J., Soler, M., Perez-Contreras, T., Aragon, S. & Moller, A. P. 1999. Antagonistic antiparasite defenses: nest defense and egg rejection in the magpie host of the great spotted cuckoo. *Behavioral Ecology*, **10**, 707–713.

Tewksbury, J. J., Martin, T. E., Hejlm, S. J., Kuehn, M. J. & Jenkins, J. W. 2002. Parental care of a cowbird host: caught between the costs of egg-removal and nest predation. *Proceedings of the Royal Society B*, **269**, 423–429.

Trnka, A. & Prokop, P. 2012. The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. *Animal Behaviour*, **83**, 263–268.

Uyehara, J. C. & Nairns, P. M. 1995. Nest defense by willow flycatchers to brood parasitic intruders. *Condor*, **97**, 361–368.

Webster, M. S. 1994. Interspecific brood parasitism of Montezuma oropendolas by giant cowbirds: parasitism or mutualism? *Condor*, **96**, 794–798.

Welbergen, J. A. & Davies, N. B. 2008. Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. *Animal Behaviour*, **76**, 811–822.

Welbergen, J. A. & Davies, N. B. 2009. Strategic variation in mobbing as a front line of defense against brood parasitism. *Current Biology*, **19**, 235–240.

Wiley, J. W. 1988. Host selection by the shiny cowbird. *Condor*, **90**, 289–303.

Zar, J. H. 1999. *Biostatistical Analysis*. 4th edn. London: Prentice Hall.