CAN NEST PREDATION EXPLAIN THE LACK OF DEFENSES AGAINST COWBIRD BROOD PARASITISM IN THE RUFOUS-COLLARED SPARROW (*ZONOTRICHIA CAPENSIS*)?

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Abstract.—Although interspecific avian brood parasitism usually lowers host productivity, some species lack any defense against parasites. We analyzed the effect of parasite egg removal or nest desertion following a parasitism event on the breeding productivity of the Rufous-collared Sparrow (*Zonotrichia capensis*), a common host of the Shiny Cowbird (*Molothrus bonariensis*). The Rufous-collared Sparrow is an effective cowbird host that does not eject parasite eggs. We removed cowbird eggs from nests of Rufous-collared Sparrows to test for differences in hatching, fledging, and nesting success among naturally unparasitized, parasitized, and experimentally unparasitized nests from which we removed the cowbird eggs. We also used simulations to test whether parasite egg removal or nest desertion provide viable strategies to counter the effects of parasitism in this species. Naturally unparasitized nests produced more nestlings and fledglings than parasitized and experimentally unparasitized nests, but there were no differences between parasitized nests and those from which cowbird eggs were removed. Moreover, the overall nesting success was similar for all nest types. Simulation models confirmed these results but also showed that productivity may still increase through parasite egg ejection when the nest predation rate is relaxed only if no cost of parasite egg ejection is assumed. By contrast, nest desertion was not a viable strategy to reduce the effect of parasitism. We suggest that high nest predation could reduce the benefits of antiparasite defenses in the Rufous-collared Sparrow and may help explain the lack of such behavior in this species. *Received 3 September 2012, accepted 4 June 2013.*

Key words: antiparasite defenses, brood parasitism, coevolution, *Molothrus bonariensis*, Rufous-collared Sparrow, Shiny Cowbird, *Zonotrichia capensis*.

¿Puede la Depredación de Nidos Explicar la Falta de Defensas de *Zonotrichia Capensis* Contra el Parasitismo de Cría de *M. bonariensis*?

Resúmen.—A pesar de que el parasitismo de cría interespecífico usualmente reduce la productividad de las especies hospedadoras, algunas de estas especies carecen de defensas contra los parásitos. En este trabajo analizamos el efecto que la remoción de huevos de los parásitos de cría y la deserción del nido siguiendo un evento de parasitismo podrían tener sobre la productividad de *Zonotrichia capensis*, una especie hospedadora común de *Molothrus bonariensis*. Esta especie es un hospedador efectivo de *M. bonariensis* y no rechaza los huevos del parásito de su nido. Realizamos la remoción de los huevos del parásito de nidos de *Z. capensis*, y comparamos el éxito de eclosión, de volantoneo y de nidificación de nidos naturalmente no parasitados, nidos parasitados y aquellos donde realizamos la remoción del huevo parásito. Además, utilizamos modelos de simulación para evaluar si la remoción de huevos del parásito y la deserción del nido podrían constituir estrategias viables para reducir los efectos del parasitismo de cría en esta especie. Los nidos naturalmente no parasitados produjeron más pichones y volantones que los nidos experimentales o los parasitados, pero no existieron diferencias entre estos dos últimos tipos de nidos. Además, el éxito de nidificación fue similar para los distintos tipos de nidos. A pesar de la falta de diferencias detectada en el experimento a campo, los modelos de simulación demostraron también que, cuando la tasa de depredación de nidos es menor, la productividad puede aún incrementarse si *Z. capensis* rechaza los huevos del parásito siempre y cuando no exista un costo en el comportamiento de rechazo. En cambio, la deserción del nido no fue una estrategia viable para reducir el impacto del parasitismo. Sugerimos que la alta tasa de depredación de nidos podría reducir los beneficios de las defensas antiparasitarias en *Z. capensis* y puede contribuir a explicar la falta de ellas en esta especie.

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Interspecific brood parasitism is a reproductive strategy in which birds lay eggs in the nests of another species that raise the parasitic offspring (Payne 1997, Rothstein and Robinson 1998). Parasitized hosts pay various fitness costs, such as egg loss when their own eggs are removed or punctured by the parasite (Sealy 1992, Mermoz and Reboreda 1994, Massoni and Reboreda 1998, Payne and Payne 1998, Clotfelter and Yasukawa 1999, Peer and Bollinger 2000, Hoover 2003). In addition, the remaining eggs may have reduced hatching success (Røskaft et al. 1990, Petit 1991, McMaster and Sealy 1998, Trine 2000, Hoover 2003), and nestlings may be more likely to die (King 1973a, Marvil and Cruz 1989, Hauber 2003, Hoover 2003, Duré Ruiz et al. 2008). As a consequence, parasitized nests usually produce fewer host fledglings.

The fitness costs associated with brood parasitism among frequently parasitized hosts are expected to select for the evolution of antiparasite defenses that prevent or reduce these costs (Rothstein 1990, Rothstein and Robinson 1998). Hosts can recognize and attack parasitic birds to prevent them from gaining access to the nest (Robertson and Norman 1976; Briskie et al. 1992; Neudorf and Sealy 1992, 1994), and they may recognize and eject parasitic eggs (Rothstein 1982, Rohwer and Spaw 1988, Sealy 1995, Sealy and Bazin 1995, Peer et al. 2000). Hosts may also recognize and discriminate against the hatched parasitic young by deserting the nest or preferentially feeding their own young (Lichtenstein 2001, Langmore et al. 2003, Grim 2007). In some cases, hosts are physically incapable of ejecting parasite eggs even though they can be recognized (Guigueno and Sealy 2012), and they opt instead for nest desertion when parasitized. Nest desertion is considered an active defense mechanism against parasitism (Rothstein 1976, Graham 1988, Hosoi and Rothstein 2000, Budnik et al. 2001, Guigueno and Sealy 2012). Despite the fitness costs associated with parasitism, a number of hosts have not evolved defenses to counteract the negative effects of parasites despite suffering a high frequency of nest parasitism (Rothstein 1975).

The Rufous-collared Sparrow (*Zonotrichia capensis*; hereafter "sparrow") is a widely distributed Neotropical species that is a major host of the brood-parasitic Shiny Cowbird (*Molothrus bonariensis*; hereafter "cowbird") in Argentina and Brazil (Friedmann 1929; King 1973a; Fraga 1978, 1983; Cavalcanti and Pimentel 1988; Fernández and Duré Ruiz 2007) that can successfully raise cowbird young (King 1973a; Fraga 1978, 1983; Fernández and Duré Ruiz 2007). Despite a high cowbird parasitism rate, sparrows lack any defense against parasitism; they do not remove cowbird eggs of any morph (immaculate or spotted eggs) or practice egg burial. The absence of antiparasite defenses is puzzling, but a previous study suggested that the high nest predation in this species would help reduce the effect of cowbird parasitism on sparrow productivity (Fernández and Duré Ruiz 2007). A high nest predation rate can prevent the development of antiparasite defenses in the host from reducing differences in reproductive success between individuals that possess these defenses and those that do not (Fernández and Duré Ruiz 2007).

Here, we analyze whether the existence of antiparasite defenses could improve the sparrow's nest productivity. First, we used field experiments to test the potential benefits of antiparasite defenses on nest productivity by performing cowbird egg removal from parasitized nests emulating parasite egg recognition and ejection, and analyzing the effect of egg removal on the breeding success and productivity of sparrows. Furthermore, we used simulation models to assess whether the productivity of a potential population of "ejectors" (individuals that recognize and eject parasite eggs) would be higher than that of a population of "acceptors" (individuals that accept parasite eggs into their nests). Because egg ejection could depend on the morphological characteristics of birds (Guigueno and Sealy 2012), we assumed an alternative scenario in which sparrows, although capable of recognizing parasite eggs, cannot eject them but opt instead for nest desertion when parasitized. Although there is no clear evidence that sparrows desert nests when they are parasitized (Fraga 1978, 1983; Mason 1985; Fernández and Duré Ruiz 2007), we used the simulation to assess whether nest desertion could enable parasitized hosts to increase reproductive success by renesting. Therefore, in this system, in which nest predation causes the failure of most nests, we expected (1) that the benefits of antiparasite defenses would be reduced; and (2) that productivity, measured as the number of fledglings produced by individuals with antiparasite defenses, would be similar or lower than for "acceptors."

Methods

Study species.—The sparrow is a socially monogamous and highly territorial species that inhabits grasslands and open woodlands from southern Mexico to Tierra del Fuego, Argentina. In our study area, it is a year-round resident and one of the most abundant passerine species. Reproductive activities appear to begin early in the season (August) at this latitude, with males singing and defending territories (Fraga 1978). Nesting activities have been documented in late September and early October and continued into early February (Fraga 1978, 1983; Mason 1985; Fernández and Duré Ruiz 2007). Sparrows build open-cup nests on or near the ground, beneath grasses, and near the bases of trees, fallen branches, and tree cavities (Fraga 1978, Mason 1985, Fernández and Duré Ruiz 2007). Clutch size is typically 3 eggs (range: 2–4; Fraga 1978, 1983; Mason 1985), incubation requires 12–13 days, and the nestling period is 9–11 days (Miller and Miller 1968, Fraga 1978, Mason 1985). Once fledged, nestlings remain in the parental territory for 20–30 days (Miller and Miller 1968, Fraga 1978). Following a successful nesting attempt, the breeding pair may make a second or even a third attempt in a season (Davis 1971, King 1973b, Fraga 1978). Cowbird parasitism at our study site (see below) occurs in 30–75% of sparrow nests, and 56% of these nests host >1 parasite egg (mode = 1 egg, range: 1–7 eggs; G. J. Fernández unpubl. data).

Study site and general procedures.—The study was carried out in an 8-ha native woodland at General Lavalle (36°20′S, 56°54′W), Buenos Aires, Argentina. The woodland is composed mainly of *Celtis tala*, *Scutia buxifolia*, *Schinus longifolius*, and *Jodina rhombifolia*. During the 2007–2011 breeding seasons (October–January), we searched for nests systematically and monitored adult activity. Nest locations were recorded using GPS (eTrex Legend, Garmin, Olathe, Kansas), and we marked nest locations in the field with an inconspicuous coded tag placed near the nest. Nest stage (building, egg laying, incubation, or nestling rearing) was noted on the date when found.

We searched for nests from early October to early January every year. Although the breeding season of sparrows extends up to February at this latitude (see above), the sampling period included the peak of the nesting attempts (Fraga 1978) and

overlapped broadly with the breeding season of the cowbird at this latitude (October–January; Fraga 1978, Mermoz and Reboreda 1994). Most nests were checked every 2–4 days (mode = 2 days; 25–75% quartiles: 2–5 days) until the young fledged or the nest failed. We considered a nest parasitized when it had ≥1 cowbird egg or nestling. On each nest visit, we recorded the number of sparrow eggs or nestlings and the number of cowbird eggs or nestlings. All eggs were inspected for cracks or punctures. Nests that lost all eggs or nestlings were assumed to have been depredated.

Experimental design and data analysis.—We removed cowbird eggs from 32 parasitized nests found during egg laying or early incubation, simulating the existence of the ability to recognize and reject cowbirds eggs. Nests where we removed cowbird eggs were selected randomly, but with the modification that we avoided removing cowbird eggs from more than two sparrow nests that we found consecutively. We also avoided removing cowbird eggs from nests where none or only one host's egg remained. When ≥1 cowbird egg was present in a nest, we removed the eggs on successive days to avoid nest desertion.

We estimated egg and nestling survival for naturally unparasitized, naturally parasitized, and experimentally unparasitized nests where we removed cowbird eggs. Egg survival was estimated using the Mayfield exposure method (Mayfield 1975). Daily egg mortality rate (DEMR) was calculated as the number of eggs lost during egg laying or incubation divided by the total number of days that those eggs remained under observation. When we did not know the exact day the egg was lost, we assumed that egg loss occurred halfway through the successive visits to the nest (Mayfield 1975). When the length of the interval between successive visits exceeded 5 days (25% of all nest checks), we applied the Johnson correction (Johnson 1979) and considered that the egg loss occurred at 40% of the length of the interval. Egg survival probability was estimated as $(1 - DEMR)^t$, where $t = 15$ days (the number of days to lay and incubate a clutch). We used the equation developed by Johnson (1979) to estimate the variance (V) of the daily egg survival rates (S): $V = [(ND - losses) \times losses]/ND^3$, where ND is the number of days that eggs were exposed, and losses refer to the number of eggs that were lost. A similar procedure was used to estimate fledging success. In this case, DNMRs were estimated as the number of nestlings lost during the nestling rearing stage divided by the number of days that they remained under observation. The probability of a nestling fledging successfully was estimated as $(1 - DNMR)^t$ ($t = 11$ days, the length of the nestling period). We used the program CONTRAST (Hines and Sauer 1989) to compare daily survival rates of eggs and nestlings among parasitized, naturally unparasitized, and experimentally unparasitized nests. CONTRAST is a general program for the post hoc comparison of multiple estimates of survival rate that incorporate the associated variance and covariance estimates (Hines and Sauer 1989).

We compared clutch size, egg losses, and the hatching success of sparrows in unparasitized, parasitized, and experimentally unparasitized nests. For the comparison of clutch sizes, we included only nests that were found during the egg-laying stage. To compare egg losses during the egg stage (egg laying + incubation), we included nests that had ≥3 eggs and that remained active >5 days under observation, regardless of the stage of incubation when found. Hatching success was calculated as the ratio of the number of young

hatched to the number of eggs present at the end of incubation. Clutch size, number of eggs at the onset of incubation, number of hatchlings, and number of fledglings produced were compared among unparasitized, parasitized, and experimentally unparasitized nests using generalized linear mixed models. In the models, nest status (unparasitized, parasitized, and experimentally unparasitized) was included as a fixed factor, and year was introduced as a random factor. We assumed a Poisson error distribution and used a logarithmic link function. We assessed the significance of factors through testing the change in the model fit when we removed them from the model (Crawley 2007).

We also estimated survival probability of entire nests for each group (unparasitized, parasitized, and experimentally unparasitized) using Mayfield's exposure method (Mayfield 1975). Daily nest mortality rates (DMRs) were estimated for the egg and nestling periods separately as the ratio between the number of nests lost during egg or nestling periods divided by the total number of days that those nests were under observation in the corresponding stage (nest losses per nest day). The daily survival rates during the egg stage (S'_{egg}) and nestling stage (S'_{nest}) were defined as $1 - DMR$. As before, when exact dates of nest loss were unknown, we assumed that failure occurred midway between successive nest visits (Mayfield 1975) and applied the Johnson correction (Johnson 1979) when the length of the interval exceeded 5 days (see above). We also used the equation developed by Johnson (1979) to estimate the variance (V) of the daily survival rates (S') as before, but now ND was the number of days that a nest remained exposed and "losses" referred to the number of nests that were lost. Nest survival probability was estimated as the product of the survival probability during the egg stage and the nestling stage (Mayfield 1975). These probabilities were each calculated as $(1 - DMR)^t$, where t is the length, in days, of the respective nesting stage (15 days for egg stage, and 11 days for the nestling rearing stage; Fernández and Duré Ruiz 2007). We assumed that daily mortality rates were constant within each nesting stage (Mayfield 1975, Johnson 1979). We used the program CONTRAST (Hines and Sauer 1989) to compare daily survival rates among unparasitized, parasitized, and experimentally unparasitized nests.

Model simulation.—We built simulation models to evaluate whether cowbird egg rejection through nest desertion or cowbird egg removal would affect sparrow productivity. To obtain more reliable estimators of breeding parameters and variables for the models, we used data obtained by G.J.F. in previous breeding seasons (2005–2006) for unparasitized and parasitized nests.

We used the following model to estimate nest productivity for unparasitized, parasitized, and experimentally unparasitized nests (those where we removed cowbird egg[s]): $F = C_s.[\gamma]^{t_h}.e.[\varphi]^{t_p}.p_h.p_p$, where F is productivity of a breeding attempt; C_s is modal clutch size (3 eggs); γ is daily egg survival rate; e is hatching success; φ is daily nestling survival rate; t_h and t_p are the lengths, in days, of the egg and nestling stage, respectively; and p_h and p_p are the probability of nest survival during the egg and nestling rearing stages, respectively. The parameters p_h and p_p were randomly generated on each simulation, assuming a Bernoulli distribution $B(p)$, where p represents the probability of survival during the egg and nestling stages, calculated on the respective DMRs. Therefore, these parameters take only values of 1 or zero (success or fail). Further, γ and φ were randomly generated

using a normal distribution with the mean equal to the daily egg or nestling survival rate for each treatment, and variance based on Johnson estimator (see above). Once γ and ϕ were selected for a nest, they remain constant for the entire period, both t_h and t_p. Also, e was randomly generated assuming a normal distribution with mean and variance estimated from observed hatching success for each nest within the different treatments (unparasitized, parasitized, and experimentally unparasitized).

We performed one simulation to compare the breeding performance of individuals that recognize and eject parasitic eggs (ejectors), individuals that accept parasitic eggs (acceptors), and individuals that desert the nest when parasitized (deserters). Also, parasite egg ejection was simulated under two alternative scenarios: (1) there is no cost of parasite egg ejection, and (2) there is a cost derived from recognition errors or the probability of damaging their own eggs when the host ejects the parasite egg. In this last situation, we assumed that the sparrow would be a puncture-ejector because its bill is <16 mm long (Rohwer and Spaw 1988, Rasmussen et al. 2010).

For all simulations, we assumed that nests had a probability of being parasitized by cowbirds w, which represent the mean parasitism rate observed in the seven breeding seasons of our study (see Table 1). Then, for each nest, we simulated the probability of being parasitized assuming a Bernoulli distribution $B(w)$, taking values equal to 1 (parasitized) or zero (unparasitized). According to these values, egg survival, hatching success, and nest predation probabilities were adjusted for each breeding attempt for unparasitized and acceptors. Nests of ejectors took egg survival, hatching success, and nest predation probability values corresponding to those observed in unparasitized sparrow nests. For simulations in which we assumed that individuals might make recognition errors or damage their own eggs when ejecting the parasite egg, we assumed that the probability of mistakenly ejecting or breaking a single host egg was 0.25, the mean value suggested for puncture-ejectors (Lorenzana and Sealy 2001). Therefore, the probability that a parasitized nest lost a host egg was simulated assuming a Bernoulli distribution $B_{(0.25)}$, where nests with a value of 1 lost 1 host egg.

A total of 12 breeding attempts (representing 3 breeding attempts during an arbitrarily defined 4-year life span) for 100 breeding individuals that recognize and eject parasitic eggs (ejectors), 100 breeding individuals that accept parasitic eggs (acceptors),

and 100 breeding individuals that desert the nest when parasitized (deserters) were simulated. We allowed deserters to make one additional breeding attempt in each breeding season if any nesting attempt was parasitized by cowbirds. Productivity values, calculated as the sum of the host fledglings produced in the 12 nesting attempts (or as much as 16 nesting attempts in the case of deserters), were compared using a Kruskal-Wallis test and *a posteriori* contrasts.

We also used a simulation model to portray a potential situation where nest predation pressure was relaxed. Simulation was conducted in a similar way as described above, but probability of nest survival equaled 0.1, 0.2, 0.3, 0.4, and 0.6. We compared productivity (number of fledglings produced after 3 or 4 nesting attempts) of acceptors, ejectors, and deserters using a Kruskal-Wallis test and *a posteriori* contrasts.

Results

We found 118 sparrow nests, 53 of which were parasitized by cowbirds (45%). We removed parasite eggs from 32 (experimentally unparasitized nests). Initial host clutch size did not differ among parasitized, unparasitized, and experimentally unparasitized nests (Wald = 0.31, df = 2 and 62.8, P = 0.86; Fig. 1), with a modal clutch size of 3 host eggs in all cases. However, the number of eggs present at the beginning of incubation differed among the three nest types (Wald = 11.82, df = 2 and 82.7, P = 0.004) because parasitized and experimentally unparasitized nests lost more host eggs than unparasitized nests before incubation started (Kruskal-Wallis, *a posteriori* comparisons, P < 0.05). Egg losses were caused by punctures to eggs by cowbirds. The number of host nestlings that hatched was also lower for parasitized and experimentally unparasitized nests than for unparasitized nests (Wald = 25.14, df = 2 and 31.9, P < 0.001; Fig. 1). However, when we included the number of eggs present at the nests at the start of incubation as an offset, the differences disappeared (Wald = 1.79, df = 2 and 30.3, P = 0.42), indicating that differences in the number of host nestlings were mainly a consequence of differences in the number of host eggs present at the nests. The number of host fledglings produced by naturally unparasitized nests also tended to be higher than those produced by parasitized and experimentally unparasitized nests, although differences were

Table 1. Breeding parameters of naturally unparasitized, parasitized, and experimentally unparasitized nests of Rufous-collared Sparrows used in the model simulations. For the simulations, we included data from previous breeding seasons to estimate the model parameters. The experimentally unparasitized nests were nests parasitized by cowbirds from which the parasitic eggs were experimentally removed.

		Unparasitized	Parasitized	With cowbird egg removal
Sample size		71	38	32
Probability of brood parasitism			0.44 (range: 0.35–0.7)	
DSR [a]	Egg	0.994 ± 0.005	0.976 ± 0.02	0.988 ± 0.01
(mean ± SE)	Nestling	0.998 ± 0.002	1	1
NSP [b]	Egg	0.23	0.31	0.39
	Nestling	0.37	0.29	0.21
Host hatching success (mean ± SE)		0.88 ± 0.03	0.51 ± 0.12	0.90 ± 0.06

[a] Daily survival rate, estimated according to the Mayfield method (see text).

[b] Nest survival probability, estimated from daily nest survival rates calculated according the Mayfield method (see text).
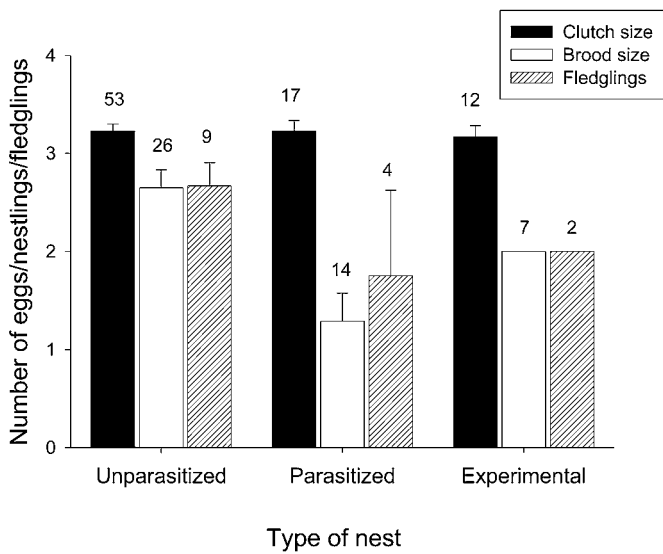
FIG. 1. Mean (± SE) numbers of eggs laid (clutch size), chicks hatched (brood size), and fledglings produced by unparasitized, parasitized, and experimentally unparasitized nests of Rufous-collared Sparrows. The experimentally unparasitized nests were nests parasitized by cowbirds from which the parasitic eggs were experimentally removed. Numbers at tops of bars are numbers of nests included in the estimation.
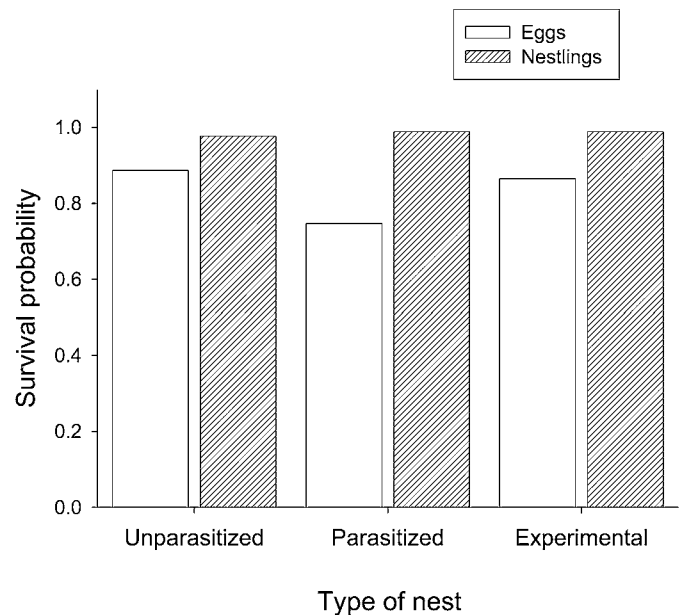

FIG. 2. Probability of nest survival of unparasitized, parasitized, and experimentally unparasitized nests of Rufous-collared Sparrows. The experimentally unparasitized nests were nests parasitized by cowbirds from which the parasitic egg was artificially removed.

only marginally significant (Wald = 7.86, df = 2 and 7.7, P = 0.06). When we included the number of nestlings hatched, differences again disappeared (Wald = 5.12, df = 2 and 7.4, P = 0.12), indicating that differences were the consequence of differences in host brood size.

In accordance with the results obtained in the regression models, daily egg survival rates differed among nest types (χ^2 = 7.93, df = 2, P = 0.02). Naturally unparasitized nests had a higher daily egg survival probability than parasitized ones (χ^2 = 7.39, df = 1, P = 0.007). Eggs of experimentally unparasitized nests did not differ in daily survival rate from eggs of naturally unparasitized (χ^2 = 1.09, df = 1, P = 0.30) or parasitized nests (χ^2 = 2.23, df = 1, P = 0.14). Daily nestling survival probabilities could not be compared because parasitized and experimentally unparasitized nests did not have any nestling mortality (none from 12 and 5 nests, respectively), and only 1 natural unparasitized nest suffered brood reduction.

Of 101 sparrow nests, 15 produced fledglings (14.8%), 74 were apparently depredated (73.3%; all nest contents disappeared), and 12 (11.9%) were abandoned. An additional 17 nests were excluded from the data set: 2 nests were deserted after the researcher visited the nest, 4 nests were destroyed by cattle, and 11 nests had unknown fates (because of logistical problems, these were not revisited).

Parasitized nests tended to be deserted more frequently than naturally unparasitized and experimentally unparasitized nests (χ^2 = 5.30, df = 2, P = 0.07). Five parasitized nests (22.7%) were deserted, 4 of them after multiple parasitism events and egg punctures to host eggs caused by cowbirds. For unknown reasons, 1 experimentally unparasitized nest and 6 natural unparasitized

nests were abandoned (3.1% and 10.1%, respectively). All the nests that failed from causes other than nest predation were excluded from the analysis of nest success to test specifically the effect of nest predation on the breeding success of each nest type. The daily nest survival rates did not differ among parasitized, naturally unparasitized, and experimentally unparasitized nests during either the incubation or nestling periods (χ^2 = 2.25, df = 2, P = 0.33; and χ^2 = 0.79, df = 2, P = 0.67, respectively; Fig. 2), and the mean nest survival probability (i.e., the probability that a nest survived until fledging) was 0.14.

Model simulations.—Table 1 summarizes the values taken by the model parameters. Simulations assuming the observed nest survival probability (0.14) showed that there were no differences in the lifetime reproductive success of ejectors and acceptors, but ejectors produced a higher number of fledglings than deserters (Kruskal-Wallis test, H = 15.62, df = 3, P < 0.001; *a posteriori* contrasts, P = 0.01, for ejectors vs. deserters; Fig. 3).

Under different simulated nest-success probabilities, nest desertion was consistently the poorest antiparasite defense because deserters produced fewer numbers of fledglings than ejectors and acceptors. Also, parasite egg ejection when individuals commit recognition errors or damage their own egg during ejection does not offer a net benefit to the host, because error-prone ejectors produced a similar number of fledglings as acceptors (P > 0.6; Fig. 3). By contrast, egg ejection without recognition errors or damage to the host's egg proved to be an effective defense against parasitism, because error-free ejectors produced significantly more fledglings than acceptors when the nest survival probability was >0.20 (Kruskal-Wallis test, *a posteriori* comparisons, P < 0.01; Fig. 3).
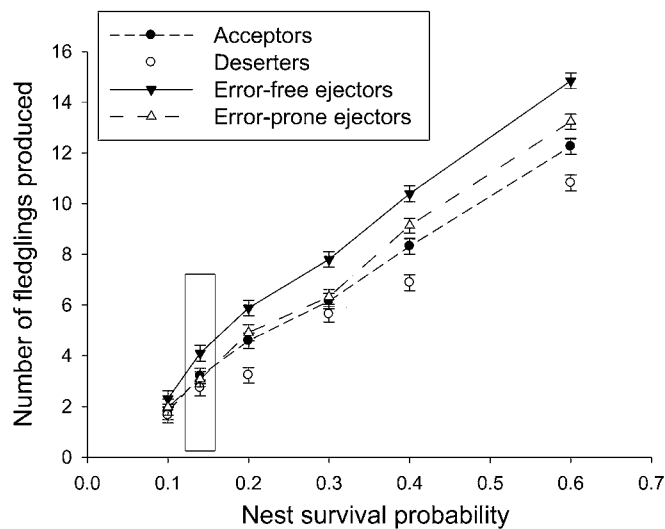
Fig. 3. Mean (± SD) number of fledglings produced, according to simulation models assuming that the population is composed of individuals that are able to recognize and eject parasite eggs without committing recognition errors (error-free ejectors), individuals that recognize and eject parasite eggs but commit recognition errors or damage their own eggs when ejecting the parasite egg (error-prone ejectors), individuals that are unable to eject the parasite egg (acceptors), and individuals that deserted the nest following cowbird parasitism (deserters). The boxed area between a nest survival probability of 0.1 and 0.2 denotes the actual mean nest survival probability from our study population ($p_{tot} = p_h \cdot p_p = 0.14$; see text). The number of fledglings produced differed significantly among antiparasite strategies except when nest survival probability was low (= 0.10).

Discussion

As with other studies performed on the Rufous-collared Sparrow (King 1973a; Fraga 1978, 1983; Fernández and Duré Ruiz 2007), parasitized nests produced a lower number of nestlings and fledglings than unparasitized nests. This effect was generated mainly by the existence of differences in the number of eggs present at the end of incubation, which was attributed to cowbird egg-pecking behavior. This result and the relatively high rate of parasitism that this species suffers (35–75 %; see above) suggest that the parasitism costs are substantial in this species, and that the lack of defenses cannot be attributable to the existence of a low cost of parasitism. Under this scenario, the sparrow should have evolved an adaptive antiparasite strategy.

The experimental data failed to support the hypothesis that parasite egg recognition and removal is an effective and viable strategy to reduce the effects of brood parasitism in the sparrow. The hatching and fledging success of nests in which we removed cowbirds eggs were similar to those of parasitized nests. This result is not totally surprising, given that one of the main costs suffered by hosts of the cowbird is egg puncture, which occurs before or during the parasitism event (Mermoz and Reboreda 1994, Massoni and Reboreda 1999, Reboreda et al. 2003). On the other hand, nest desertion was also associated with cowbird parasitism, but this behavior is likely a response to an abnormal clutch size due to multiple parasitism events (i.e., the nest received >1 cowbird egg), to egg

losses due to egg punctures (Rothstein 1975; Fraga 1978, 1983), or to disturbance resulting from increased activity of cowbirds at the nest, rather than constituting a specific antiparasite response.

Simulation models confirmed our results. Although recognizing and ejecting the parasite egg could increase the number of fledglings that a bird can rear, the high probability of nest predation means that the parasite-egg-ejection behavior did not generate any benefit in terms of productivity, particularly when individuals can make egg-recognition errors or damage their own eggs during ejection. On the other hand, simulations also revealed that desertion of parasitized nests did not improve individual productivity, because the number of fledglings produced was lower than for acceptors. These results appear to support the hypothesis that this species' nest failure rate could reduce the effect of brood parasitism (Fernández and Duré Ruiz 2007) and increase the cost of renesting. However, simulations considering a slightly higher nest survival probability than that observed in the field, and assuming no cost of parasite egg ejection, produced a different result. In this case, error-free ejectors produced a higher number of fledglings than acceptors or deserters. Therefore, under this scenario, cowbird-egg recognition and ejection could constitute an adaptive and efficient antiparasite strategy that should be favored by natural selection as long as there are no costs of rejection. Therefore, the evolution of antiparasite defenses in the sparrow could depend on the nest predation rates that this host suffers. In our study, nest survival probability ranged from 8% to 16%, values similar to those reported in other studies of this species (Mason 1985, Fraga 1978, Lazo and Anabalon 1992). Only King (1973b) reported higher nesting success (34%), for a population of sparrows at Horco Molle (Tucumán, Argentina). However, nest predation rates can vary widely depending on environmental variations (Cox et al. 2012) and, in turn, could produce similar variation in the costs and benefits that antiparasite defenses could give to a host. We think that this variation could explain, in addition to the possible existence of rejection costs, the lack of defenses in the sparrow.

Simulations also assumed that costs of parasitism were restricted to the reduction in host productivity. However, the presence of a parasite nestling could affect the host's nestling development and adult parental effort, reducing the host's offspring recruitment and adult survival (Dearborn et al. 1998, Hoover and Reetz 2006). Given these costs, cowbird-egg ejection could still constitute an adaptive strategy if it improved the host's offspring or adult survival. These effects, however, still depend on the frequency with which the host's nests become parasitized and then survive long enough to produce fledglings. When nest predation rates are elevated, this probability is reduced and, consequently, so are the benefits derived from the antiparasite defense.

Coevolutionary implications.—Usually, lack of defenses in a host is interpreted as being due to the existence of an evolutionary lag in the origin and spread of antiparasite adaptations ("evolutionary lag hypothesis"; Rothstein 1975, 1990) or the existence of additional costs in the evolution of host defenses ("equilibrium hypothesis"; Rohwer and Spaw 1988, Lotem et al. 1992, Lotem and Nakamura 1998). The lag hypothesis explains the lack of defenses in parasite–host systems with a relatively recent coevolutionary history (Payne 1997, Rothstein and Robinson 1998). In the case of the sparrow and the cowbird, we presumed that they have a relatively long coexistence because they have an apparently similar Neotropical origin (Zink et al. 1991, Lanyon and Omland 1999) and occupy a similar broad range of habitats, from grassland to open woodlands (King

1974, Lowther and Post 1999). This coexistence can be dated to 0.8–1.2 mya, from the origin and expansion of the cowbird in South America (Rothstein et al. 2002). Additionally, species that coexist with the sparrow and are usual hosts of cowbirds have evolved the recognition and ejection of parasite eggs as antiparasite defenses. For example, the Rufous Hornero (*Furnarius rufus*) and Red-crested Cardinal (*Paroaria coronate*) recognize and eject cowbird eggs from parasitized nests (Mason and Rothstein 1986, Massoni et al. 2012, Segura and Reboreda 2012), and the Chalk-browed Mockingbird (*Mimus saturninus*) and Rufous-bellied Thrush (*Turdus rufiventris*) reject parasite eggs of the white morph (Sackmann and Reboreda 2003). This evidence led us to speculate that sparrows may have had sufficient time to evolve antiparasite defenses if such defenses were strongly favored by selection.

An alternative hypothesis proposes that there are morphological or ecological constraints that would explain the lack of defenses in some hosts (Krüger 2011). These constraints result in an evolutionary equilibrium whereby the costs of the evolution of antiparasite defenses exceed the benefits. The sparrow is likely too small to grasp-eject the parasite egg (Rohwer and Spaw 1988, Rasmussen et al. 2010); furthermore, most puncture-ejecting hosts are also larger than sparrows (but see Sealy 1996). If neither of these antiparasite defenses is possible, nest desertion would be the only option that nesting birds have to respond to parasitism by cowbirds. As we showed in the simulations, there is no adaptive advantage of nest desertion following parasitism, because any new nesting attempt will have a high probability of being parasitized and/or will have a low probability of success. Therefore, an apparent evolutionary lag is generated because of the tradeoff between the costs and benefits of the antiparasite strategies (Krüger 2011). It is possible that additional costs associated with antiparasite strategies such as recognition errors and the accidental breakage of a bird's own eggs when trying to eject a parasite egg (Lotem et al. 1992, Lotem and Nakamura 1998), as well as passive benefits such as a dilution effect generated by the presence of parasite eggs in the nest (Gloag et al. 2012), could make the evolution of antiparasite defenses unlikely.

In short, the high nest predation rate that sparrows suffer could be seen as a constraint in the coevolution of this parasite–host system, and the lack of defenses in the host can be interpreted as the result of a reduction of the brood parasitism costs because of this high nest predation rate. Similar arguments could be applied to other cowbird hosts in which imperfect defenses or the lack of defenses have been observed (Mermoz and Reboreda 1994, Massoni and Reboreda 1998, Mermoz and Fernández 1999, Sackmann and Reboreda 2003, Astié and Reboreda 2005). In that sense, the host's response to parasitism should not be seen merely as a consequence of the coevolutionary history and the intensity and effects of parasitism, but it is likely to depend on the host's life-history parameters and ecological constraints such as nest predation rates.

Acknowledgments

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