

SHORT COMMUNICATION

Host switching in cowbird brood parasites: how often does it occur?

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Abstract

Avian obligate brood parasites lay their eggs in nests of host species, which provide all parental care. Brood parasites may be host specialists, if they use one or a few host species, or host generalists, if they parasitize many hosts. Within the latter, strains of host-specific females might coexist. Although females preferentially parasitize one host, they may occasionally successfully parasitize the nest of another species. These host switching events allow the colonization of new hosts and the expansion of brood parasites into new areas. In this study, we analyse host switching in two parasitic cowbirds, the specialist screaming cowbird (*Molothrus rufoaxillaris*) and the generalist shiny cowbird (*M. bonariensis*), and compare the frequency of host switches between these species with different parasitism strategies. Contrary to expected, host switches did not occur more frequently in the generalist than in the specialist brood parasite. We also found that migration between hosts was asymmetrical in most cases and host switches towards one host were more recurrent than backwards, thus differing among hosts within the same species. This might depend on a combination of factors including the rate at which females lay eggs in nests of alternative hosts, fledging success of the chicks in this new host and their subsequent success in parasitizing it.

Introduction

Obligate brood parasitism is a breeding strategy used by 100 avian species (Davies, 2000) and consists of parasites laying their eggs in nests of other species, the hosts, completely avoiding investment in parental care. Co-evolutionary interactions between parasites and their hosts have resulted in amazing adaptations where the former mimic host eggs (Brooke & Davies, 1988; Moksnes & Røskaft, 1995; Antonov *et al.*, 2010; Stoddard & Stevens, 2010) and chick morphology (Sorenson *et al.*, 2003; De Mársico *et al.*, 2012), and the latter, in

turn, evict parasites' eggs (Davies & Brooke, 1988; Rothstein, 1990; Davies, 2000; Peer & Sealy, 2004; Grim *et al.*, 2011; Kilner & Langmore, 2011) or chicks (Langmore *et al.*, 2003; Grim, 2007; Tokue & Ueda, 2010; De Mársico *et al.*, 2012) to overcome the costs imposed by parasitism. Host-specific adaptations to increase parasitism success occur in host-specialist parasites (Sorenson *et al.*, 2003; De Mársico *et al.*, 2012) but also in host generalists where strains of host-specialist females coexist (Gibbs *et al.*, 2000; Spottiswoode *et al.*, 2011). In these species, speciation is prevented by random mating among individuals raised by different hosts (Marchetti *et al.*, 1998; Spottiswoode *et al.*, 2011; but see Fossey *et al.*, 2011). It has been suggested that host-specific adaptations within the same species arise by a preference for a particular host and maternally transmitted adaptive characters (Gibbs *et al.*, 2000; Spottiswoode *et al.*, 2011). Host preference seems to be

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mediated by an imprinting process during chick period, when individuals create an association with host parents (Brooke & Davies, 1991; Payne *et al.*, 1998, 2000), nest site (Moksnes & Røskaft, 1995) or habitat (Teuschl *et al.*, 1998) and afterwards parasitize these nests when adults. However, females may occasionally parasitize nests of an alternative host. When imprinting occurs in both parasite males and females, like in African indigo-birds (*Vidua* spp.), mislaying of eggs leads to sympatric speciation (Sorenson *et al.*, 2003), but when host specialization is limited to females, these host-switching events generate new host-specific maternal lineages (Davies, 2000). Although in at least one parasite species host switching is extremely rare (Spottiswoode *et al.*, 2011), it is frequent in several other brood parasites (Gibbs *et al.*, 2000; Sorenson *et al.*, 2003; Mahler *et al.*, 2007, 2009). In some of these species, host-switching allowed the colonization of new hosts and the subsequent expansion of the parasite's distribution area (Ortega, 1998).

The aim of this study was to estimate how often host switching takes place in two species of New World brood parasitic cowbirds (Passeriformes: Icteridae) with different parasitism strategies. One of the seven independent evolutionary origins of obligate brood parasitism occurred in this group of birds (Lanyon, 1992) which comprises five species that differ in their parasitism strategies, with the extremes represented by the screaming cowbird (*Molothrus rufoaxillaris*), the most specialized parasite of the group, and the shiny cowbird (*M. bonariensis*) which is, along with the brown-headed cowbird (*M. ater*), highly generalist (Lowther, 2014). The screaming cowbird has been thought to use a single host species, the baywing (*Agelaioides badius*, Friedmann, 1929, 1963), evolving mimetic chick plumage and calls to deceive this host (Hudson, 1874; Fraga, 1979, 1998; De Mársico *et al.*, 2012). However, in the last years, recordings of two new host species, the chopi blackbird (*Gnorimopsar chopi*, Sick, 1985; Fraga, 1996; Di Giacomo & Reboreda, 2015) and the brown-and-yellow marshbird (*Pseudoleistes virescens*, Mermoz & Reboreda, 1996; Mermoz & Fernández, 2003), have been documented in some parts of its distribution. The shiny cowbird, on the other hand, uses more than 250 hosts (Ortega, 1998; Lowther, 2014), of which 98 successfully raise parasitic chicks (Lowther, 2014). Although host use differs at population level, previous studies found evidence of host preference at individual level for both species, with females selectively choosing the nests of only some of the available hosts (López-Ortiz *et al.*, 2006; De Mársico *et al.*, 2010). Genetic studies on mtDNA haplotype frequency distribution (Mahler *et al.*, 2007, 2009) supported the existence of host-specific female lineages but also revealed that haplotypes were not unique to one host species, indicating host switches by brood parasitic females.

Differences in parasitism strategies among molothrine brood parasites have been related to differences in their imprinting process (Ellison *et al.*, 2006). For host-specific species, stronger imprinting would limit parasitism to a few hosts. In contrast, host generalists might change host more often due to a softer imprinting process that favours more frequent host switches. Furthermore, colonization of new hosts allowed these species spreading into habitats that became suitable by deforestation, agriculture and livestock activities, thereby considerably expanding their distribution (Ortega, 1998). Host switching also greatly affects host-parasite dynamics by relaxing the parasite's density dependence on host abundance (Ney-Nifle *et al.*, 2005).

The preference of female lineages for parasitizing one host species generates a nonrandom distribution of their molecular markers among hosts, as females carrying the same mtDNA haplotype (i.e. belonging to the same lineage) use the same host (Gibbs *et al.*, 2000). Occasionally, females successfully use the nest of another species (Moksnes & Røskaft, 1995; Nakamura & Miyazawa, 1997; Marchetti *et al.*, 1998; De la Colina, 2013). These host switching events lead to the presence of the same haplotype in different hosts. Thus, we estimate the frequency of host switching in both cowbird species based on mtDNA haplotype distribution. By treating females that preferentially use different host species as separate host-specific populations, we estimate the number of migrants per generation as a measure of host switching females. Nuclear markers were not used as host specificity is limited to females, which are assumed to mate with males reared by any host species (Gibbs *et al.*, 1997, 2000; Marchetti *et al.*, 1998; Spottiswoode *et al.*, 2011; but see Fossøy *et al.*, 2011). We analyse host-switching for both the specialist screaming cowbird and the generalist shiny cowbird and examine whether host switching occurs more frequently in the generalist brood parasite, favouring the colonization of numerous hosts. We also compare shiny cowbirds' host switching in two different host communities and determine whether they vary depending on host species.

Materials and methods

We studied the frequency at which host switching occurs for one population of screaming cowbirds and two populations of shiny cowbirds that use different host communities (Table 1). The screaming cowbird population was studied at 'Reserva El Bagual', Formosa Province, Argentina (26°10' S, 58°56' W), where it uses two host species, the baywing and the chopi blackbird. Genetic data were taken from Mahler *et al.* (2009). For shiny cowbirds, mtDNA haplotype distribution was analysed for one population at 'Estancia El Destino', Magdalena, Buenos Aires Province, Argentina (35°08' S, 57°23' W), where it mainly parasitizes chalk-browed mockingbird (*Mimus saturninus*) and house wren

(*Troglodytes aedon*) nests, although other host species are used at lower frequencies (Mason, 1986). This population was genetically studied by Mahler *et al.* (2007). The other shiny cowbird population was studied at the same location as the screaming cowbird and genetic data is presented in this paper. Samples for this latter study were collected in Formosa during 2008 and 2009 breeding seasons (October–December). We collected eggs and blood samples of 6- to 9-day-old nestlings found in nests of two hosts, the rufous hornero (*Furnarius rufus*) and the golden-winged cacique (*Cacicus chrysopterus*). Both species are the main hosts of the shiny cowbird in this area, with parasitism frequencies of 59% in the rufous hornero and 54% in the golden-winged cacique and parasitism intensities of 1–4 cowbird eggs per parasitized nest in the former and 1–9 eggs in the latter (Di Giacomo, 2005).

Genetic analyses were based on a 1120-bp fragment of mtDNA control region and performed following Mahler *et al.* (2007). New nucleotide sequences have been deposited in the EMBL, GenBank, under accession numbers JN226129–JN226142. A median-joining network (Bandelt *et al.*, 1999) showing haplotype relationships was constructed using NETWORK V 4.612 (<http://www.fluxus-engineering.com>) (Fig. 1). We estimated the minimum number of changes (host-switches) needed to explain haplotype distribution among hosts (Sorenson *et al.*, 2003) by treating ‘host’ as a character and considering the initial use of one host by the ancestral (= more frequent and central; Avise, 2000) haplotype (H7) and assuming that identical mitochondrial sequences did not originate independently in different lineages by parallel evolution. We analysed population structure between host use with AMOVA and the exact test of population differentiation as implemented in ARLEQUIN V 3.11 (Excoffier *et al.*, 2005). To minimize the possibility of including multiple

offspring of the same female, we discarded egg samples that shared the same haplotype and had the same coloration pattern ($N = 1$). Individual females lay constant egg types, with similar background colour and spotting pattern (Fleischer, 1985; Lyon, 1997; De la Colina, 2013; Gloag *et al.*, 2014). We assumed that dissimilar eggs were laid by different females and similar eggs by the same female. Blood samples sharing haplotype with any sample were considered to belong to different females when they were collected with a considerable spatial separation (> 3 km), taking into account that females have a limited laying area (De la Colina, 2013; Scardamaglia & Reboreda, 2014). Multiple offspring that might belong to the same female were excluded from the analysis ($N = 1$).

To analyse host switching, we estimated migration rates based on mtDNA haplotype distribution between chicks found in the nests of different hosts (Fig. 1). We considered cowbird samples collected from each host’s nests to belong to one host-specific population and performed gene flow analysis between populations with the software MIGRATE V 3.2.16 (Beerli & Felsenstein, 1999). Thus, migrants are equivalent to host switchers.

We analysed gene flow between host populations for the three data sets separately using Bayesian inference. This coalescence method uses a probabilistic model that can handle different immigration rates and different population sizes, therefore outperforming F_{st} -based approaches (Beerli & Felsenstein, 2001). Moreover, estimates are not affected by nonsampled populations, which in our case would correspond to other host species (Beerli, 2004). A Metropolis–Hastings Markov chain Monte Carlo method estimates the migration rate $M = N_{ef} m$, where N_{ef} is the effective female population size and m is the number of migrants per generation. We estimated host-specific population size as the number of females using each particular host.

Based on the results of previous studies, we estimated the number of active females using each host (N_{ef}). Parasitism frequencies and intensities vary geographically for the same host species (De Mársico *et al.*, 2010), but remain fairly constant in one area (Reboreda *et al.*, 2013). This indicates that population size, and consequently number of laying females, does not vary between consecutive reproductive seasons. For the shiny cowbird population sampled by Mahler *et al.* (2007) in Buenos Aires, we estimated the number of laying females based on three studies carried out in this area. Based on a genetic egg-assignment analysis of De la Colina (2013), the mean number of eggs laid by a female within the sampling area was estimated in 4.26 (SE = 1.97). Dividing the number of collected eggs per breeding season per host (Mean: 117.5 ± 6.4 eggs in mockingbird and 20.5 ± 3.5 eggs in wren nests) by 4.26, we calculated the number of laying females which resulted in 28 for mockingbirds and five for house wrens. For the remaining area that was also included

Table 1 Cowbird populations included in host switching analyses. In parentheses, female effective population sizes are shown (see text).

| Brood parasitic species | Screaming cowbird | Shiny cowbird | |
|---------------------------|--------------------------------|----------------------------------|-------------------------------|
| Strategy | Host specialist | Host generalist | |
| Location | Formosa | Formosa | Buenos Aires |
| Host 1 (N_{ef}) | <i>Agelaioides badius</i> (18) | <i>Furnarius rufus</i> (37) | <i>Troglodytes aedon</i> (12) |
| Host 2 (N_{ef}) | <i>Gnorimopsar chopi</i> (16) | <i>Cacicus chrysopterus</i> (13) | <i>Mimus saturninus</i> (69) |
| ϕ_{st} between hosts | 0.05*† | 0.05*‡ | 0.23**§ |

†Mahler *et al.* (2009).

‡This study.

§Mahler *et al.* (2007).

Significance as determined in studies * $P < 0.05$, ** $P < 0.001$.

Results

For the shiny cowbird population in Formosa, there was a significant difference in haplotype frequency distribution between hosts (AMOVA: $\Phi_{ST} = 0.052$, $P = 0.027$; Exact test: $P = 0.012$), indicating host preference at individual level as was found for the Buenos Aires population by Mahler *et al.* (2007). Analyses were based on 18 different haplotypes of 46 samples taken from two hosts' nests (rufous hornero $N = 25$ and golden-winged cacique $N = 21$; Fig. 1). Although individual host preference is evidenced by nonrandom haplotype distribution between hosts, seven host switching events can be identified in the haplotype network (Fig. 1).

Estimates of gene flow obtained with MIGRATE software are shown in Fig. 2. The number of migrants per generation was not higher in the generalist brood parasite compared to the more specialist brood parasite (mean \pm SD.: shiny cowbird 0.12 ± 0.07 vs. screaming cowbird 0.135 ± 0.04). The number of migrants per generation was related to host species and was asymmetrical in the majority of the cases (Fig. 2).

Discussion

In this study, we present an original contribution and a new perspective of the widely studied avian brood parasitism. Although evidence of female host-specific lineages has been presented in previous studies (Marchetti *et al.*, 1998; Gibbs *et al.*, 2000; Sorenson *et al.*, 2003; Mahler *et al.*, 2007, 2009; Spottiswoode *et al.*, 2011), this is the first study analysing the frequency at which host switching events by parasitic females occur among different hosts.

Two previous studies (Mahler *et al.*, 2007, 2009) and data presented in this article analysed genetic differentiation in mtDNA haplotype frequency distribution between cowbird chicks found in nests of different hosts and revealed genetic differentiation but also shared haplotypes among hosts used, indicating individual host preference together with occasional host switches by brood parasitic females. We estimated host switching as the migration rates per generation between different hosts for one screaming cowbird and two shiny cowbird populations. Unexpectedly, we found that rates at which host switching occur are not very different between the generalist and the specialist brood parasite. As parasitism of many hosts and use of new species are prevalent in the shiny cowbird, we expected more frequent host switches in this species. However, we found that the number of migrants per generation between both hosts of the specialist screaming cowbird was not lower than that observed in the generalist brood parasite. We also found that host switching is asymmetrical and that it might occur more frequently in the direction of one host than of the other. In consequence, the rate at which host switching occurs is dependent on host species.

Theoretical analysis has suggested that one migrant per generation typically prevents genetic differentiation among populations (Wright, 1931; Slatkin, 1985). The number of cowbird females that incur in host switching is below this threshold, thus retaining host-specific lineages in both cowbird parasite species. Like in the Common Cuckoo (*Cuculus canorus*) (Gibbs *et al.*, 2000), the rate of host switching is low over ecological time, taking years to occur, but is sufficiently frequent over evolutionary times so as to hamper a perfect association of mtDNA lineages with host species.

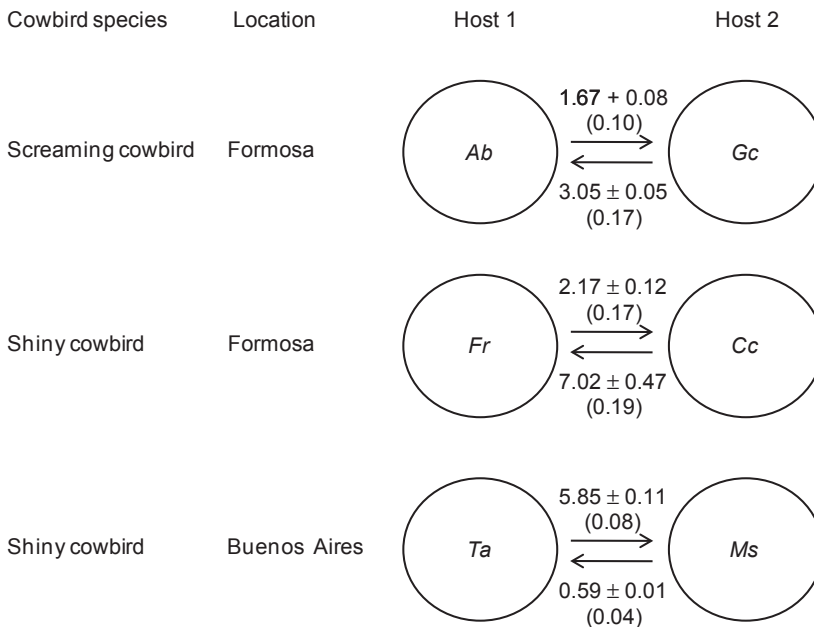


Fig. 2 Migration rate $M \pm SD$ and number of migrants (= host switching females) per generation m (in parentheses) between hosts of three different communities. Values are shown above and below arrows indicating the direction of migration. Letters inside circles stand for host species: Ab: Baywing (*Agelaioides badius*), Gch: chopi blackbird (*Gnorimopsar chopi*), Fr: rufous hornero (*Furnarius rufus*), Cc: golden-winged cacique (*Cacicus chrysopterus*), Ta: house wren (*Troglodytes aedon*), Ms: chalk-browed mockingbird (*Mimus saturninus*).

One question that arises is why nests of alternative hosts are used when individual females have a preference for one host species. Di Giacomo *et al.* (2010) proposed that laying in nests of a different species could be the result of recognition errors, based on their records of screaming cowbird parasitism in species that nested close to the preferred host. Another explanation for the use of an alternative host's nest is social learning, where a female follows another female during nest searching (De Mársico *et al.*, 2010). A recent study in shiny cowbirds showed that several females may collectively approach a nest and successively lay their eggs (Gloag *et al.*, 2014). Multiple parasitism by shiny cowbirds in one nest at the same day has been reported before (Mermoz & Rebores, 1999), but this new evidence shows that laying by several females is practically simultaneous. Thus, females might use other female's information to find nests and, in some cases, follow females raised by different hosts. Recent findings support this explanation as they show that the majority of shiny cowbird females parasitize only one host species, but some of them parasitize an alternative host at low frequencies (De la Colina, 2013). Although laying in a host different than the preferred one was observed for several females in one breeding season (De la Colina, 2013), the proportion of cases where this effectively constitutes a migration event is low. On the one hand, this egg has to successfully hatch and fledge. Puncture behaviour by other parasitic females, as well as high predation rates, gives a very low fledging success: 0.12–0.17 in screaming cowbirds (Di Giacomo & Rebores, 2015) and 0.03–0.28 in shiny cowbirds (Fiorini *et al.*, 2005). On the other hand, a successfully raised female will have to leave offspring in this new host to give rise to a new lineage, which will spread with her daughters leaving successful descendants in this host, in turn. This process might explain the pattern that we found in both brood parasitic species, where the frequency of host switching was not significantly higher in the generalist brood parasite. Differences in fledging success between parasites might be related to factors such as puncture behaviour of parasite females, rejection of nonmimetic eggs by hosts and the success of hosts in rearing parasitic offspring.

Differences in fledging success might also account for the differences in host switching among hosts of the same brood parasite. Alternatively, if social learning guides laying behaviour, the rate at which females occasionally parasitize a different host might be associated with the number of females using each of them, with a higher migration rate towards the host used by more females. Interestingly, we found that the number of migrants per generation (host switching females) was always higher for the scarcer variety of females. Migration towards mockingbirds ($N_{ef} = 69$) was higher than towards wrens ($N_{ef} = 12$) in the shiny cowbird population of Buenos Aires; in Formosa, it was higher

towards the rufous hornero ($N_{ef} = 37$) than in the direction of caciques ($N_{ef} = 13$), and for the screaming cowbird, migration was higher towards baywings ($N_{ef} = 18$) than towards chopi blackbirds ($N_{ef} = 16$). A parasitic female may follow conspecific females to increase her chances of parasitism when she was not successful during the previous day in finding a suitable nest to parasitize (De Mársico *et al.*, 2010). If the majority of females are using a particular host, this increases the probability of a given female to end up parasitizing that same host.

Finally, unequal migration rates might be a consequence of host imprinting (Ellison *et al.*, 2006). Mahler *et al.* (2007) suggested that hosts with the same nest type are used indiscriminately by females, whereas they seldom use hosts with another nest type. It is possible that diverse or particular cues make parasitism in some alternative hosts more frequent than in others. This, in turn, will affect the number of migrants using these new hosts. Moreover, host-specific adaptations can be a barrier to host switching and thus prevent migration between hosts. For example, in the case of the greater honeyguide (*Indicator indicator*), no recent host switches were observed between hosts nesting in tree cavities and hosts nesting in terrestrial burrows (Spottiswoode *et al.*, 2011).

In sum, we show that successful 'colonization' of another host species, leading to a new host-specific lineage, is variable among parasites and among hosts within one parasite species. Host switching events will depend on a combination of factors including the rate at which females lay eggs in nests of alternative hosts, fledging success of the chicks in this new host and their subsequent success in parasitizing it. This ability to switch to new hosts is widespread among brood parasites and is a fundamental requirement for their expansion into new areas.

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References

- Antonov, A., Stokke, B.G., Vikan, J.R., Fossøy, F., Ranke, P.S., Røskaft, E. *et al.* 2010. Egg phenotype differentiation in sympatric cuckoo *Cuculus canorus* gentes. *J. Evol. Biol.* **23**: 1170–1182.

- Avise, J.C. 2000. *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, MA.
- Bandelt, H.J., Forster, P. & Röhl, A. 1999. Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* **16**: 37–48.
- Beerli, P. & Felsenstein, J. 1999. Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. *Genetics* **152**: 763–773.
- Beerli, P. & Felsenstein, J. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. *Proc. Natl. Acad. Sci. USA* **98**: 4563–4568.
- Beerli, P. 2004. Effect of unsampled populations on the estimation of population sizes and migration rates between sampled populations. *Mol. Ecol.* **13**: 827–836.
- Brooke, M. de L. & Davies, N.B. 1988. Egg mimicry by cuckoos, *Cuculus canorus*, in relation to discrimination by hosts. *Nature* **335**: 630–632.
- Brooke, M. de L. & Davies, N.B. 1991. A failure to demonstrate host imprinting in the cuckoo (*Cuculus canorus*) and alternative hypotheses for the maintenance of egg mimicry. *Ethology* **89**: 154–166.
- Davies, N.B. 2000. *Cuckoos, Cowbirds and Other Cheats*. T. & A. D. Poyser, London.
- Davies, N.B. & Brooke, L. 1988. Cuckoos versus Reed Warblers: adaptations and counter adaptations. *Anim. Behav.* **36**: 262–284.
- De la Colina, M.A. 2013. Estudio a nivel individual de las estrategias de parasitismo del Tordo Renegrido (*Molothrus bonariensis*). Ph.D. thesis, Central Library Dr. Luis Federico Leloir, University of Buenos Aires, Argentina.
- De Mársico, M.C., Mahler, B. & Reboreda, J.C. 2010. Reproductive success and nestling growth of Bay-winged cowbirds parasitized by Screaming and Shiny Cowbirds. *Wilson J. Ornithol.* **122**: 417–431.
- De Mársico, M.C., Gantchoff, M.G. & Reboreda, J.C. 2012. Host-parasite coevolution beyond the nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. *Proc. Biol. Sci.* **279**: 3401–3408.
- Di Giacomo, A.G. 2005. Aves de la Reserva El Bagual. In: *Historia natural y paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina* (A.G. Di Giacomo & S.F. Krapovickas, eds), pp. 426–430. Aves Argentinas/Asociación Ornitológica del Plata, Buenos Aires.
- Di Giacomo, A.G. & Reboreda, J.C. 2015. Reproductive success of the specialist brood parasite Screaming Cowbird in an alternative host, the Chopi Blackbird. *Auk* **132**: 16–24.
- Di Giacomo, A.G., Mahler, B. & Reboreda, J.C. 2010. Screaming Cowbird parasitism on nests of Solitary Caticues and Cattle Tyrants. *Wilson J. Ornithol.* **122**: 795–799.
- Ellison, K., Sealy, S.G. & Gibbs, H.L. 2006. Genetic elucidation of host use by individual sympatric Bronzed Cowbirds (*Molothrus aeneus*) and Brown-headed Cowbirds (*M. ater*). *Can. J. Zool.* **84**: 1269–1280.
- Excoffier, L., Laval, G. & Schneider, S. 2005. Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evol. Bioinform. Online* **1**: 47–50.
- Fiorini, V.D., Astié, A.A., Tuero, D.T. & Reboreda, J.C. 2005. Éxito reproductivo del Tordo Renegrido, *Molothrus bonariensis*, en hospedadores de distinto tamaño corporal. *Hornero* **20**: 173–182.
- Fleischer, R.C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. *Behav. Ecol. Sociobiol.* **17**: 91–100.
- Fossey, F., Antonov, A., Moksnes, A., Røskaft, E., Vikan, J.R., Møller, A.P. et al. 2011. Genetic differentiation among sympatric cuckoo host races: males matter. *Proc. R. Soc. Lond. B* **278**: 1639–1645.
- Fraga, R.M. 1979. Differences between nestlings and fledglings of screaming and bay-winged cowbirds. *Wilson Bull.* **91**: 151–154.
- Fraga, R.M. 1996. Further evidence of parasitism of chopi blackbirds (*Gnorimopsar chopi*) by the specialized screaming cowbird (*Molothrus rufoaxillaris*). *Condor* **98**: 866–867.
- Fraga, R.M. 1998. Interactions of the parasitic screaming and shiny cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the bay-winged cowbird (*M. badius*). In: *Parasitic Birds and Their Hosts: Studies in Coevolution* (S.I. Rothstein & S.K. Robinson, eds), pp. 173–193. Oxford University Press, New York.
- Friedmann, H. 1929. *The Cowbirds: A Study in the Biology of Social Parasitism*. C. Thomas Publisher, Springfield, IL.
- Friedmann, H. 1963. Host relations of the parasitic cowbirds. *Bull. U. S. Natl. Mus.* **233**: 1–276.
- Gibbs, H.L., Miller, P., Alderson, G. & Sealy, S.G. 1997. Genetic analysis of brown-headed cowbirds *Molothrus ater* raised by different hosts: data from mtDNA and microsatellite DNA markers. *Mol. Ecol.* **6**: 189–193.
- Gibbs, H.L., Marchetti, K., Sorenson, M.D., Brooke, M.de.L., Davies, N.B. & Nakamura, H. 2000. Genetic evidence for female host-specific races of the common cuckoo. *Nature* **407**: 183–186.
- Gloag, R., Fiorini, V.D., Reboreda, J.C. & Kacelnik, A. 2014. Shiny cowbirds share nests, but not mothers, in multiply parasitized mockingbird broods. *Behav. Ecol. Sociobiol.* **68**: 681–689.
- Grim, T. 2007. Experimental evidence for chick discrimination without recognition in a brood parasite host. *Proc. R. Soc. B* **274**: 373–381.
- Grim, T., Samás, P., Moskát, C., Kleven, O., Honza, M., Moksnes, A. et al. 2011. Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? *J. Anim. Ecol.* **80**: 508–518.
- Hudson, W.H. 1874. Notes on the procreant instincts of three species of *Molothrus* found in Buenos Ayres. *Proc. Zool. Soc. Lond.* **42**: 153–174.
- Kilner, R.M. & Langmore, N.E. 2011. Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. *Biol. Rev.* **86**: 836–852.
- 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.
- Lanyon, S. 1992. Interspecific brood parasitism in blackbirds (Icterinae): a phylogenetic perspective. *Science* **255**: 77–79.
- López-Ortiz, R., Ventosa-Febles, E.A., Ramos-Alvarez, K.R., Medina-Miranda, R. & Cruz, A. 2006. Reduction in host use suggests host specificity in individual shiny cowbirds (*Molothrus bonariensis*). *Ornitol. Neotrop.* **17**: 259–269.
- Lowther, P.E. 2014. Lists of victims and hosts of the parasitic cowbirds. Available at <http://www.fieldmuseum.org/sites/>

- default/files/plowther/2014/09/24/cowbird_hosts-17sep2014.pdf. Accessed October 14, 2014.
- Lyon, B.E. 1997. Spatial patterns of shiny cowbird brood parasitism on chestnut-capped blackbirds. *Anim. Behav.* **54**: 927–939.
- Mahler, B., Confalonieri, V.A., Lovette, I.J. & Reboreda, J.C. 2007. Partial host fidelity in nest selection by the shiny cowbird (*Molothrus bonariensis*), a highly generalist avian brood parasite. *J. Evol. Biol.* **20**: 1918–1923.
- Mahler, B., Sarquis Adamson, Y., Di Giacomo, A., Confalonieri, V. & Reboreda, J.C. 2009. Utilization of a new host in the screaming cowbird (*Molothrus rufoaxillaris*), a host specialist brood parasite: host switch or host acquisition? *Behav. Ecol. Sociobiol.* **63**: 1603–1608.
- Marchetti, K., Gibbs, H.L. & Nakamura, H. 1998. Host-race formation in the common cuckoo. *Science* **282**: 471–472.
- Mason, P. 1986. Brood parasitism in a host generalist, the Shiny Cowbird. II. Host selection. *Auk* **103**: 61–69.
- Mermoz, M.E. & Reboreda, J.C. 1996. New effective host for the Screaming Cowbird. *Condor* **98**: 630–632.
- Mermoz, M.E. & Reboreda, J.C. 1999. Egg-laying behaviour by shiny cowbirds parasitizing brown-and-yellow marshbirds. *Anim. Behav.* **58**: 873–882.
- Mermoz, M.E. & Fernández, G.J. 2003. Breeding success of a specialist brood parasite, the Screaming Cowbird, parasitizing an alternative host. *Condor* **105**: 63–72.
- Moksnes, A. & Røskaft, E. 1995. Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *J. Zool.* **236**: 625–648.
- Nakamura, H. & Miyazawa, Y. 1997. Movements, space use and social organisation of radio-tracked common cuckoos during the breeding season in Japan. *Jap. J. Ornithol.* **46**: 23–54.
- Ney-Nifle, M., Bernstein, C., Reboreda, J.C. & Kacelnik, A. 2005. Population dynamics and avian brood parasitism: persistence and invasions in a three species system. *J. Anim. Ecol.* **74**: 274–284.
- Ortega, C. 1998. *Cowbirds and Other Brood Parasites*. University of Arizona Press, Tucson.
- Payne, R.B., Payne, L.L. & Woods, J.L. 1998. Song learning in brood-parasitic indigobirds *Vidua chalybeata*: song mimicry of the host species. *Anim. Behav.* **55**: 1537–1553.
- Payne, R.B., Payne, L.L., Woods, J.L. & Sorenson, M.D. 2000. Imprinting and the origin of parasite–host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. *Anim. Behav.* **59**: 69–81.
- Peer, B.D. & Sealy, S.G. 2004. Correlates of egg rejection in hosts of the brown-headed cowbird. *Condor* **106**: 580–599.
- Reboreda, J.C., Fiorini, V.D. & De Mársico, M.C. 2013. Antiparasitic defences in hosts of South American cowbirds. *Chin. Birds* **4**: 57–70.
- Rothstein, S.I. 1990. A model system for coevolution: avian brood parasitism. *Annu. Rev. Ecol. Syst.* **21**: 481–508.
- Scardamaglia, R. & Reboreda, J.C. 2014. Ranging behavior of female and male Shiny and Screaming Cowbirds while searching for host nests. *Auk* **131**: 610–618.
- Sick, H. 1985. *Ornitologia Brasileira, uma introducao*. Universidade de Brasilia, Brasilia, Brazil.
- Slatkin, M. 1985. Gene flow in natural populations. *Ann Rev Ecol Syst* **16**: 393–430.
- Sorenson, M.D., Sefc, K.M. & Payne, R.B. 2003. Speciation by host switch in brood parasitic indigobirds. *Nature* **424**: 928–931.
- Spottiswoode, C.N., Stryjewski, K.F., Quader, S., Colebrook-Robjent, J.F.R. & Sorenson, M.D. 2011. Ancient host-specificity within a single species of brood parasitic bird. *Proc. Natl. Acad. Sci. USA* **108**: 17738–17742.
- Stoddard, M.C. & Stevens, M. 2010. Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proc. R. Soc. B* **277**: 1387–1393.
- Teuschl, Y., Taborsky, B. & Taborsky, M. 1998. How do cuckoos find their hosts? The role of habitat imprinting. *Anim. Behav.* **56**: 1425–1433.
- Tokue, K. & Ueda, K. 2010. Mangrove gerygones *Gerygone laevigaster* eject little bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. *Ibis* **152**: 835–839.
- Tuero, D.T., Fiorini, V.D. & Reboreda, J.C. 2007. Effects of shiny cowbird *Molothrus bonariensis* parasitism on different components of house wren *Troglodytes aedon* reproductive success. *Ibis* **149**: 521–529.
- Wright, S. 1931. Evolution in Mendelian Populations. *Genetics* **160**: 97–159.

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