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Host Use by Generalist and Specialist Brood-Parasitic Cowbirds at Population and Individual Levels

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I. Introduction

Interspecific brood parasitism is a breeding strategy in which some individuals (the parasites) lay eggs in nests of individuals of other species (the hosts) that provide parental care to parasitic offspring (Davies, 2000; Payne, 1977; Rothstein and Robinson, 1998). Interspecific brood parasitism has evolved independently at least seven times in birds (Sorenson and Payne, 2002): three times among the cuckoos (family Cuculidae), once among the honeyguides (family Indicatoridae), once among waterfowl (black-headed duck, *Heteronetta atricapilla*), and two times among songbirds, one in the African brood-parasitic finches (family Viduidae) and the other in the cowbirds (genus *Molothrus*, family Icteridae).

Brood parasitism reduces the reproductive success of the host (Rothstein and Robinson, 1998), which selects for the evolution of antiparasitic defenses in the host and potentially creates a coevolutionary arms race between hosts and parasites (Krüger, 2007; Rothstein, 1990). Coevolutionary theory predicts that brood parasites will become more specialized the longer they are in contact with a particular avifauna (Davies and Brooke, 1989; Rothstein, 1990). This happens because hosts evolve defenses against parasitism, such as rejection of foreign eggs (Davies and Brooke, 1988). In turn, parasites evolve counterdefenses, such as mimicry of host eggs (Brooke and Davies, 1988). These counterdefenses are specific to a single

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host species or to a group of hosts with similar features, such as similar egg types. Because genetic constraints do not allow a single population to simultaneously maintain numerous alternative character states, such as many different mimetic egg types, parasitic birds should parasitize a smaller number of host species as time passes and as more and more potential host species evolve antiparasitic defenses (Rothstein et al., 2002).

In parasitic cowbirds, the order in which each species branched off from the rest of its lineage correlates with the number of hosts it uses (Lanyon, 1992). This has led to the conclusion that host specificity was the ancestral character in cowbirds, from which an increasing generalization in host use has evolved (Lanyon, 1992). This conclusion was criticized by some authors who argued that the current number of hosts is an evolutionary labile trait that depends more on the ecological circumstances the parasite faces than on its phylogenetic history (Rothstein et al., 2002).

Generally, the criterion to determine whether a brood parasite is a specialist or a generalist is the current number of hosts it uses at population level (i.e., if the species uses one or very few host it is a specialist, whereas if it uses many hosts it is a generalist). However, generalist brood parasites could be host specialists at individual level, with each female consistently parasitizing one particular host species. In this case, females may eventually form host-specific lineages that may evolve specific counteradaptations to evade host antiparasitic defenses (Avilés and Møller, 2004; Brooke and Davies, 1988; Starling et al., 2006). Alternatively, brood parasites could be generalists also at individual level, with each female parasitizing several host species during her lifetime. To know whether a brood parasite is specialist or generalist at individual level is important because if they are generalists, parasite's populations may be uncoupled from that of their relatively uncommon hosts and therefore may threaten their hosts' populations. In contrast, specialist parasites are less likely to drive hosts to extinction because their population dynamics are coupled to their hosts' populations (May and Robinson, 1985; Takasu et al., 1993).

Here, we will study host use in two Neotropical parasitic cowbirds that differ markedly in the degree of host specialization: the shiny cowbird (*Molothrus bonariensis*), an extreme host-generalist, and the screaming cowbird (*Molothrus rufoaxillaris*), one of the most specialized brood parasites (Ortega, 1998), to try to elucidate possible factors favoring one or the other strategy. We will address three questions related to host use and host specialization in brood-parasitic cowbirds. First, does a generalist parasite use all available hosts indistinctly or does it exhibit some preference for certain species within and across host communities? Second, why does a specialist brood parasite not use other potentially suitable hosts? And third, are cowbird females host-specialist or host-generalist at individual level?

A. Host Use by Shiny Cowbirds at Population Level

The shiny cowbird is an extreme generalist brood parasite. Its eggs have been found in nests of nearly 250 hosts and 93 of them have successfully reared cowbird young (Lowther, 2009; Ortega, 1998). These hosts possess a wide range of body masses, from 10 to 80 g. Shiny cowbirds are omnivorous ground foragers that feed in conspecific or mixed flocks and are sexually dimorphic in plumage and body mass (males: 51 g, females: 47 g; Reboreda et al., 1996). The shiny cowbird is the most widespread species of cowbird. They were originally confined to open and semiopen areas of South America and Trinidad and Tobago, but they expanded through the Caribbean during 1901–1982 and invaded North America in 1987, incorporating new host species during this expansion (Ortega, 1998). Very little is known about factors influencing community patterns of host use by shiny cowbirds. This information is scarce because data on parasitism are usually gathered by studying a particular host species, without simultaneously collecting information about the availability of other suitable hosts within the bird community and the extent to which they are used by shiny cowbirds. To understand host use by shiny cowbirds at a community level, it is necessary to analyze information originated in the same area, with appropriate nest sample sizes and including all potential hosts within the community. Two studies that have followed this approach are those of Mason (1986) and Wiley (1988). The first author studied host use by shiny cowbirds in grasslands of Argentina and concluded that cowbirds prefer to parasitize nests of passerines larger than themselves. This author also noted differences in the frequency of parasitism of the same hosts between two sites that were less than 20 km apart and interpreted these differences as a result of changes in the structure of host community (Mason, 1986). Wiley (1988) examined host use by shiny cowbirds in the mangrove community in Puerto Rico and noted that this species did not parasitize hosts in proportion to their abundances and that the cowbird's breeding season coincided with those of "high-quality" hosts (i.e., species that fledged $>55\%$ of cowbirds' hatched chicks). This author also observed that food habits and egg size of hosts were similar to those of shiny cowbirds and suggested that they chose hosts partly on the basis of these features. Similar studies conducted in the host-generalist brown-headed cowbird (*M. ater*) showed that open nesters were parasitized more often than cavity nesters and that the largest host species were never parasitized (Strausberger and Ashley, 1997), providing evidence for nonrandom laying by parasitic females.

There is some debate about whether brood parasites should use hosts smaller or larger than themselves. In hosts larger than the parasite, the poor contact of the smaller parasite egg with the host's brood patch may prevent effective incubation (Peer and Bollinger, 1997), and larger host chicks may outcompete parasitic chicks for food (Lichtenstein, 1998; Scott and Lemon, 1996). Alternatively, smaller hosts deliver less food to the nest, which may result in lower growth rate and longer exposure to nest predation of the parasitic chicks. Regarding the use of hosts with open or closed nests, open nests may be easier to find and to access, but species with open nests may have higher predation rates than those with closed nests (Martin and Li, 1992).

B. Host Use by Screaming Cowbirds at Population Level

The screaming cowbird is the most specialized parasitic cowbird (Ortega, 1998). This species is sympatric over its entire range in southern South America with the shiny cowbird, with which it overlaps broadly in habitat use (Ortega, 1998). Like shiny cowbirds, screaming cowbirds inhabit grasslands and open woodlands, and are omnivorous ground foragers that often form mixed flocks with other icterine species (Fraga, 1986). They are monomorphic in plumage (Friedmann, 1929), but males are larger than females (55–58 vs. 48–50 g, respectively; Mason, 1987, Reboreda et al., 1996). Another major difference between screaming and shiny cowbirds is that the former are usually seen in pairs, even during the nonbreeding season (De Mársico and Reboreda, 2008a; Fraga, 1986; Mason, 1987). This regular association between sexes led some authors to suggest that they are socially monogamous (Friedmann, 1929; Mason, 1987), but further studies are necessary to determine the genetic mating system of this species.

Screaming cowbirds parasitize mainly the baywing (*Agelaioides badius*; Friedmann, 1929; Hudson, 1874). This host is a sexually monomorphic, medium-sized blackbird (40 g), and it is also a secondary host of the shiny cowbird (Fraga, 1998; Mason, 1986). The frequency of screaming cowbird parasitism in baywing nests is extremely high (83–100%) and most nests are usually multiply parasitized (Fraga, 1998; Hoy and Ottow, 1964; Mason, 1980). Baywings differ from most other cowbirds' hosts in that they rarely build their own nest, but breed in a variety of domed nests built by other species and secondary cavities (Fraga, 1998; Friedmann, 1929; Hoy and Ottow, 1964). This unusual nesting behavior may be related to the fact that baywings start to breed later than most other passerines (De Mársico et al., 2010; Fraga, 1998; Friedmann, 1929; Hoy and Ottow, 1964). The breeding season of screaming cowbirds closely matches that of baywings, but parasitic females often start to lay earlier as a result of poor timing of parasitism with hosts' laying (De Mársico and Reboreda, 2008a; Fraga, 1998). The hosts' incubation period is 1 day longer than that of screaming cowbirds (13 vs. 12 days; Fraga, 1998), which added to the parasite's larger body size, provides the parasitic nestling with a head start when parasitism is properly synchronized with host's laying (De Mársico and Reboreda, 2008b; Fraga, 1998). In addition, baywings are cooperative breeders (Fraga, 1991), and the presence of helpers at the nest that contribute to chick feeding may decrease the intensity of competition for food within the brood. In support of this, brood reduction in baywings occurs rarely. Thus, it is possible that screaming cowbirds' young do not face strong competition for food in the nests of their main host (De Mársico and Reboreda, 2008b). A striking feature of young screaming cowbirds is that they exhibit a close similarity to hosts' young in plumage coloration, which persists until the parasitic fledglings molt into the adult black plumage (Fraga, 1979, 1998). This similarity cannot be explained by common ancestry (Lanyon, 1992; Lanyon and Omland, 1999), so it could be a true case of mimicry. There is some evidence indicating that baywings do not provide parental care to fledglings that do not look like their own (Fraga, 1998; Lichtenstein, 1997), but further experimental studies are needed to assess the adaptive value of chick mimicry in this host–parasite system.

In some parts of their distribution, screaming cowbirds also parasitize two other species: the chopi blackbird (*Gnorimopsar chopi*; Di Giacomo, 2005; Fraga, 1996; Sick, 1985) and the brown-and-yellow marshbird (*Pseudoleistes virescens*; Mermoz and Fernández, 2003; Mermoz and Reboreda, 1996). Like baywings, these hosts are cooperative breeders (Di Giacomo, 2005; Orians et al., 1977). The chopi blackbird lives in open woodlands, savannas, and palm grooves from northeastern Argentina and Uruguay to central Brazil (Orians, 1985). They breed in preexisting holes in trees, but may also locate their nests in human constructions (Fraga, 1996). Data on breeding biology and parasitism by screaming cowbirds in chopi blackbirds are scarce. Most available information comes from Di Giacomo (2005) and a few opportunistic observations of hosts' nesting behavior and interactions with parasites at the nest in areas where baywings were rarely seen (Fraga, 1996). Previous studies indicate that screaming cowbirds parasitize chopi blackbirds starting in early October, nests are multiply parasitized, and parasitic chicks seem to be equally successful in nests of this host and in baywing nests (Di Giacomo, 2005; Fraga, 1996). Chopi blackbirds are larger in body size than screaming cowbirds (adult body mass: ~68 g; Di Giacomo, 2005), but have a longer incubation period (14–15 days; Di Giacomo, 2005), thus screaming cowbird chicks may hatch well in advance of hosts' chicks.

The other screaming cowbird's host, the brown-and-yellow marshbird, inhabits humid grasslands and marshes in eastern Argentina, Uruguay, and Brazil, and its distribution totally overlaps that of baywings (Ridgely and Tudor, 1989). Contrary to the other screaming cowbird's hosts, brown-and-yellow marshbirds build open-cup nests on a variety of exotic and native plants at 0.5–1.5 m above ground (Mermoz and Reboreda, 1998). The frequency of parasitism is much lower than in baywings, ranging from 6% to 20% depending on the year (Mermoz and Fernández, 2003). The brown-and-yellow marshbird is also a primary host of the shiny cowbird in eastern Argentina (frequency of parasitism: 66–74%; Mermoz and Reboreda, 1994; Mermoz and Reboreda, 1998), thus nests parasitized by screaming cowbirds also often have shiny cowbird eggs (Mermoz and Fernández, 2003). Like chopi blackbirds, brown-and-yellow marshbirds are larger than screaming cowbirds (adult body mass: ~80 g; Mermoz and Reboreda, 1994), but because the host has a longer incubation period (13–15 days; Mermoz and Reboreda, 2003), parasite chicks usually hatch earlier than hosts' chicks and are rarely outcompeted by them (Mermoz and Fernández, 2003).

Host specificity in screaming cowbirds is puzzling as they co-occur with several species that could be suitable hosts. The specificity cannot be explained by the relatively late parasite's breeding season (Friedmann, 1929) or any preference for particular habitats or nest types (e.g., Teuschl et al., 1998) because the hosts currently used vary in the timing of their breeding period and cover a wide variety of nesting sites, including old nests of many species in open woodlands, cavities in trees and buildings, and open nests in marshy grasslands (Fraga, 1996, 1998; Mermoz and Fernández, 2003). Coevolutionary theory predicts that brood parasites should become more specialized over time as more hosts develop antiparasitic defenses (Rothstein et al., 2002). In this context, screaming cowbird females may avoid parasitizing host species that attack them when visiting the nest or reject their eggs. Nevertheless, there is evidence that several unparasitized species that could be suitable hosts do not have well-developed defenses against screaming cowbird females or eggs (De Mársico and Reboreda, 2008b; Mason, 1986).

Another explanation for the maintenance of host specificity is that parasite's reproductive success is lower with currently unused hosts than with the preferred ones. In support of this idea, there is experimental evidence that screaming cowbird chicks cross-fostered to unused but otherwise suitable hosts experienced higher mortality rates than in baywing nests (De Mársico and Reboreda, 2008b). Screaming cowbird chicks forced to grow in nests of a larger host, the chalk-browed mockingbird (*Mimus saturninus*), were often outcompeted by their nestmates despite being the first to hatch; chicks cross-fostered to a smaller host, the house wren (*Troglodytes aedon*), did not suffer from competition for food but from a high incidence of ectoparasites, which greatly affected chick's growth and survival (De Mársico and Reboreda, 2008b). Both death causes are almost absent in the nests of the screaming cowbird's hosts for various reasons. First, competition for food is usually improved by the earlier hatching or the larger size of screaming cowbird chicks relative to host's chicks; second, the three host species have helpers at the nest which are likely to increase overall nest provisioning rates; and finally, baywings remove ectoparasites from their own and parasitic chicks (Fraga, 1984). Altogether, these experiments and observations suggest that host use by screaming cowbirds may be limited by the ability of their chicks to survive under conditions different from those found in the preferred hosts.

C. Host Use by Shiny and Screaming Cowbirds at Individual Level

Shiny and screaming cowbirds use fewer species than those that could potentially be successful hosts. This evidence suggests that brood-parasitic cowbirds do not lay eggs randomly, but preferentially use some of the available hosts. This laying pattern at population level can, however, arise from different strategies of host use at individual level. One option is that individual females become specialists, with each female consistently parasitizing one particular host species, or, alternatively, they may become generalists, with individual females parasitizing several host species. In the first case, there would be host-specialized female groups, whereas in the second case, all females of a population would deposit their eggs in the nests of all hosts used by that cowbird population.

Indirect and direct evidence have shown that generalist brood parasites evolved different laying strategies at individual level. The Old-world common cuckoo (*Cuculus canorus*) uses over 200 species as hosts (Payne, 2005), but individual common cuckoo females use only one or a few host species, laying eggs that resemble those of the host they parasitize (Avilés and Møller, 2004; Brooke and Davies, 1988; Moksnes and Røskraft, 1995). Indirect molecular evidence, based on mitochondrial DNA (mtDNA) sequences, showed the existence of host-specific female lineages (or gentes), with host switches occurring many times along evolutionary time (Gibbs et al., 2000). Differences in mtDNA were not paralleled by nuclear markers as a consequence of male mating behavior, which is independent of host, thus preventing host-related speciation. These findings were supported by direct evidence concerning individual laying and mating patterns via microsatellite markers (Marchetti et al., 1998; Skjelseth et al., 2004). Host-specific female lineages would be maintained by females inheriting the mtDNA from their mothers and also sharing her choice of host species (Gibbs et al., 2000). Rarely, host-switching events might occur when a female lays in a host nest different from the one in which she was reared (Davies, 2000). This host-switching mechanism stemming from errors in the recognition of the host has also led to colonization of new hosts and speciation in host-specialist Vidua finches (Payne et al., 2002; Sorenson et al., 2003).

In the pallid cuckoo (*Cuculus pallidus*), indirect evidence also suggests female host-specificity (Starling et al., 2006). By analyzing several parasitized host clutches of four different species, the authors found that cuckoo eggs mimicked those of each of the hosts, similar to what has been found for the common cuckoo. This pattern arises from the coevolutionary arms race in which hosts and parasites are engaged, where hosts evolve antiparasitic defenses such as egg rejection to decrease the costs of parasitism, which in turn selects for counterdefenses such as egg mimicry in the parasite (Davies, 2000; Davies and Brooke 1989; Davies et al., 1989; Rothstein, 1990; Rothstein and Robinson, 1998). Directional selection of hosts on parasites' egg color can only occur if the latter consistently use the nests of the same species or of species showing similar egg types.

Several hypotheses have been proposed to account for host-specific laying. One mechanism that has been proposed to explain host specialization at individual level is that parasitic females imprint on their foster parents, and once mature they parasitize individuals of the same species (Brooke and Davies, 1991; Nicolai, 1964; Payne, 1973; Slagsvold and Hansen, 2001). Direct support for this hypothesis comes from experiments with brood-parasitic village indigobirds (*Vidua chalybeata*) bred in captivity and foster-reared by their normal host or by an experimental foster species. When adult village indigobird females were tested for host choice, they preferentially parasitized the species that had reared them (Payne et al., 1998, 2000). Another explanation is that females are philopatric and use the hosts present in their natal area (Brooke and Davies, 1991). Alternatively, nest site choice would lead brood-parasitic females to lay in nests of hosts with similar eggs and nest sites (Moksnes and Røskraft, 1995). Finally, there might be an imprinting of the habitat where parasitic females hatch, for which they will later search when laying their eggs (Teuschl et al., 1998; Vogl et al., 2002). However, which of these processes leads individual females to lay in the nests of a particular host species remains unclear.

Individual laying strategies have also been studied in two North-American cowbird species, the brown-headed cowbird and the bronzed cowbird (*M. aeneus*), which are closely related to our study species. The brown-headed cowbird is as generalist as the shiny cowbird with nearly 250 described hosts (Lowther, 2009). A study that analyzed host use in this species indirectly (i.e., based on mtDNA haplotypes) did not find any differentiation in haplotype frequency distribution among hosts, suggesting that females of this species use nests randomly for laying (Gibbs et al., 1997). Later studies that tested for host use directly found evidence of mixed laying behavior in female brown-headed cowbirds. These studies assigned cowbird offspring that were found in host nests to particular females through parentage analyses. A first study used DNA fingerprinting (Hahn et al., 1999) and found that females were territorial and used the nests of all available hosts within their territory, thus indicating that individual females were generalists. A couple of subsequent studies based on microsatellite DNA markers found that females of the same population used both specialist and generalist laying strategies (Alderson et al., 1999; Strausberger and Ashley, 2005; Woolfenden et al., 2003). Laying strategy in this species seems to be plastic and adjusted to environmental conditions (Woolfenden et al., 2003). However, territoriality of females is always maintained. Consistent nest site selection has been documented by the observation of females returning to a specific area during successive years (Hauber, 2001; Hoover et al., 2006). Parasitism strategies were also studied for the bronzed cowbird in an area of sympatry with the brown-headed cowbird (Ellison et al., 2006). Based on microsatellites, the authors found that both species overlapped minimally in host use, each of them having four preferred hosts. At individual level, bronzed cowbirds showed a similar laying pattern to brown-headed cowbirds, with both specialist and generalist females in the same population.

The limitation in host use at population level by shiny cowbirds is intriguing. Why do shiny cowbirds use only some of the available hosts? Are individual females using one host species or are all of them randomly using the nests of only a group of hosts employing a shotgun strategy by which the use of a great number of hosts assures that at least some of the eggs are successful (Kattan, 1997; Rothstein and Robinson, 1998)? And, why do screaming cowbirds use alternative hosts only in some areas of their distribution? We will discuss the findings of previous studies (Mahler et al., 2007, 2009) that analyzed cowbirds' mtDNA haplotype distributions among hosts giving indirect evidence on individual host use in both species.

D. OBJECTIVES

The aims of this study are: (1) to determine to what extent shiny cowbirds are generalists at a population level by analyzing community patterns of host use by this parasite in different areas of its distribution; (2) to test whether host use by shiny cowbirds is associated to some host characteristics like body mass, type of nests, or phylogenetic proximity; (3) to provide updated information on host use at population level by screaming cowbirds, including the comparison of the parasite's success in the different reported hosts; (4) to discuss the observed pattern of host use by screaming cowbirds at population level in light of previous experimental work involving cross-fostering of screaming cowbird eggs and chicks to nests of suitable but unused hosts; and (5) to analyze evidences of host use at individual level by shiny and screaming cowbirds.

II. METHODS

A. HOST USE BY SHINY COWBIRDS AT POPULATION LEVEL

1. Study Areas and Data Collection

Our study was based on data about host use by shiny cowbirds that were collected in four different sites corresponding to three biogeographic regions of Argentina: ‘‘Pampas’’ grasslands, ‘‘Espinal’’ shrublands, and humid ‘‘Chaco’’ woodlands. Data on host use by shiny cowbirds in ‘‘Pampas’’ grasslands were obtained from different studies conducted in a small region of Buenos Aires Province near the towns of Magdalena (35° 08′ S, 57° 23′ W), Chascomús (35° 34′ S, 58° 01′ W), and General Lavalle (36° 26′ S, 56° 25′ W) (De Mársico et al., 2010; Fernández and Duré Ruiz, 2007; Fernandez and Mermoz, 2000; Fiorini and Reboreda, 2006; Lyon, 1997; Mason, 1986; Massoni and Reboreda, 1998; Massoni et al., 2006; Mermoz and Reboreda, 2003; Sackmann and Reboreda, 2003; Tuero et al., 2007). Data of host use by shiny cowbirds in ‘‘Espinal’’ shrublands were obtained from two different sites: (1) near the town of Villa María (32° 24′ S, 63° 14′ W), Córdoba province (Salvador, 1983), and (2) near the town of Esperanza (31° 27′ S, 60° 56′ W), Santa Fe province (De La Peña, 2005). Because these areas are 250 km apart, these data were analyzed separately. Data on host use by shiny cowbirds in humid ‘‘Chaco’’ woodlands were obtained in Reserva El Bagual (26° 18′ S, 58° 49′ W), Formosa Province (Di Giacomo, 2005; this study). We included in our analysis only the species that had been reported previously as hosts of shiny cowbirds (Lowther, 2009) and for which we had at least five nest records. Our dataset included 21 hosts in Buenos Aires, 19 in Córdoba, 41 in Santa Fe, and 51 in Formosa. The number of nests per host was 35.2 ± 4.4 (mean ± SE, $n = 132$ hosts-sites, see Appendix I).

2. Data Analysis

For each host, we determined: (1) frequency of parasitism, (2) type of nest, (3) egg volume (as a surrogate for host's body size), and (4) genetic distance between the host and the parasite. We calculated frequency of parasitism as number of nests with parasitic eggs or chicks divided by total number of nests. Egg volume was calculated as $l \times w^2 \times x$, where l and w were the length and width of the eggs (mm), and x was a species-specific constant. The mean value of this constant for 26 species of birds is 5.07×10^{-4}

(Hoyt, 1979). Because the interspecific variation of this constant is not much greater than the intraspecific one, we used this value for all calculations of egg volume. Nest types were classified as open or closed. Closed nests included domed nests and cavities. Genetic distances between the host and the parasite were estimated using the sequences of cytochrome *b* obtained from the EMBL, GenBank. We compiled the sequences in Bioedit Version 7.0.5.3 software (Hall, 1999) and aligned them using Clustal W (Thompson et al., 1994). Genetic distances between host and parasite were calculated with the Dnadist module of the Phylip v.3.68 Package using the Kimura two-parameter model for nucleotide substitution with a transition/transversion ratio of 2.0 (Felsenstein, 2008).

3. *Statistical Analysis*

We used Spearman rank correlations to analyze the association of the frequency of parasitism with hosts' egg volume and genetic distance between the host and the parasite. We tested shiny cowbird's preferences for hosts with open or closed nests by comparing the mean frequency of parasitism of open versus closed nesters using Mann–Whitney *U* tests. We analyzed if shiny cowbirds showed consistent preferences for some hosts by analyzing the association between frequencies of parasitism on the same hosts in different places using Spearman rank correlations. For the analysis of the association between frequency of parasitism and genetic distance between the host and the parasite, we considered the different hosts as independent points (i.e., we assumed that shiny cowbirds started to parasitize them after speciation events within each clade). We used nonparametric statistics because our data were not normally distributed and the sample sizes were relatively small. All tests were two-tailed and significance was accepted at $P < 0.05$. Values presented are mean ± SE.

B. Host Use by Screaming Cowbirds at Population Level

1. *Study Areas and Data Collection*

Data on screaming cowbird parasitism were collected in two different places: Reserva de Flora y Fauna El Destino near Magdalena (35° 08′ S, 57° 23′ W) in Buenos Aires Province, and Reserva Ecológica El Bagual (26° 18′ S, 58° 49′ W) in Formosa Province. Reserva El Destino is a flat area of 320 ha located in the "Pampas" grassland, with average annual rainfall of 885 mm and mean monthly temperatures varying from 5.9 °C in July to 27.5 °C in January. Reserva El Bagual is an open savanna of 3300 ha in the eastern, humid Chaco region. Average annual rainfall is 1350 mm and mean monthly temperatures vary from 16.9 °C in July to 26.7 °C in January.

In Reserva El Destino, screaming cowbirds parasitize baywings. This host is single brooded (Fraga, 1991) and breeds in the area from late November to late February (De Mársico and Reboreda, 2008a). In Reserva El Bagual, screaming cowbirds parasitize baywings and chopi blackbirds (Mahler et al., 2009). Baywings breed in this area from mid-November to late March and chopi blackbirds breed from late October to late December (Di Giacomo, 2005). In El Destino, data were collected during the breeding seasons 2002–2003 to 2006–2007, whereas in El Bagual, data were collected during the breeding seasons 1997–1998 to 2007–2008.

We monitored 193 baywing nests in Reserva El Destino, and 69 baywing and 267 chopi blackbird nests in Reserva El Bagual. In El Destino, most baywing nests occurred in old nests of other species, but 40 nests were found in wooden nest boxes previously placed in the study area (for a detailed description, see De Mársico and Reboreda, 2008a). In El Bagual, all chopi blackbird nests were in wooden nest boxes, whereas baywing nests were found in old nests of many species (e.g., *Phacellodomus ruber*, *P. sibilatrix*, *Furnarius rufus*). Most nests were found before or during host's laying and were visited every 1–3 days until chicks fledged or the nest failed. We marked individual eggs with waterproof ink and assigned them to the host or to shiny or screaming cowbirds on the basis of background color, spotting pattern, and shape (Fraga, 1983). We identified nestlings of each species using skin and bill coloration (Fraga, 1979). We banded all host and parasite chicks at the age of 9–11 days with a unique combination of colored plastic leg bands and a numbered aluminum band to identify them out of the nest. A nest was considered successful if it fledged at least one host or parasite chick; otherwise, we considered that the nest failed.

From 2003 to 2006, we conducted cross-fostering experiments in El Destino, which involved the transfer of screaming cowbird eggs or newly hatched chicks from naturally parasitized baywing nests to nests of chalk-browed mockingbirds ($n = 54$ nests) and house wrens ($n = 33$ nests). The experimental procedure was described in detail in De Mársico and Reboreda (2008b). Similarly, we transferred shiny cowbird eggs from parasitized chalk-browed mockingbird to baywing nests in order to assess the success of shiny cowbird eggs and chicks with this secondary host. Experimental nests were checked in the same way as described above.

2. *Data Analysis*

We considered a nest parasitized if it received a parasitic egg at any stage of the host's nesting cycle. The frequency of parasitism was calculated as the number of nests parasitized divided by the number of nests found. The overall intensity of parasitism was calculated as the number of cowbird eggs laid per nest over the host's nesting cycle, considering only nests found before or during the host's laying. When the host was parasitized by screaming and shiny cowbirds, we calculated the frequency and intensity of parasitism by each species separately.

We estimated the apparent nest survival rate as the number of successful nests divided by the number of nests found before or during host's laying in which hosts began to lay. To quantify the parasite's reproductive success, we estimated hatching success and chick survival of screaming cowbirds parasitizing different host populations. Hatching success was based upon only those nests that survived until the nestling stage, and was calculated as the number of parasitic eggs that hatched relative to the number that survived until the end of incubation. Chick survival was the proportion of parasitic chicks that fledged from those that hatched in nests that survived until fledging. Whenever possible, we compared our data with those for screaming cowbirds parasitizing brown-and-yellow marshbirds near General Lavalle (36° 26′ S, 56° 25′ W), Buenos Aires Province. Data on parasitism in this host species were obtained from Mermoz and Fernández (2003).

3. *Statistical Analysis*

We used nonparametric statistics, as most of our data did not meet the assumptions of parametric tests. Statistical significance was accepted at $P < 0.05$. Values presented are mean ± SE.

C. HOST USE BY SHINY AND SCREAMING COWBIRDS AT INDIVIDUAL LEVEL

1. *Study Areas and Data Collection*

We collected tissue and blood samples of shiny cowbird's eggs and chicks, respectively, during three breeding seasons from nests of four host species at three different locations in Buenos Aires Province, Argentina, that are separated by 150 km at most: Magdalena, General Lavalle, and Chascomús (for a detailed description, see Mahler et al., 2007). Samples were collected from offspring of chalk-browed mockingbird ($n = 30$), brown-and-yellow marshbird ($n = 25$), and rufous-collared sparrow (*Zonotrichia capensis*; $n = 17$) in nests found in the study areas, and from wooden nest boxes placed in the three locations that were used by house wrens ($n = 29$). We collected samples of screaming cowbird offspring during two breeding seasons at Reserva El Bagual, Formosa Province. Samples were collected from offspring in baywing nests ($n = 27$) and from chopi blackbird offspring ($n = 31$) in wooden nest boxes (for a detailed description, see Mahler et al., 2009).

2. *Data Analysis*

We extracted DNA for subsequent mtDNA control region sequencing as described in Mahler et al. (2007, 2009). To determine host use at individual level in shiny and screaming cowbirds, we analyzed mtDNA haplotype distribution among hosts. We expected to find genetic differences among chicks reared by different hosts if individual females were host specialists and if female chicks reared in the nests of a particular host had a strong tendency to parasitize that same host as adults, whereas we expected no pattern of genetic differentiation if each female parasitized the nests of all hosts indiscriminately or if they differed in host use from their mothers. A differentiation pattern will occur as a consequence of parallel inheritance of mtDNA haplotype and host use. Females that lay their eggs in the nests of a particular host will transmit the mtDNA to their daughters and the latter will preferentially use the nests they were reared in, transmitting in turn their mtDNA to their daughters (which will be the same as their grandmother's) and so on. In that way, all descendants of the first female will share mtDNA haplotype and host use, giving origin to a host-specialized female lineage.

3. *Statistical Analysis*

Population structure based on haplotype frequencies among hosts was analyzed with the program Arlequin v.2.0 (Schneider et al., 2000). After controlling for confounding factors like multiple offspring of the same female, and in the case of shiny cowbirds, sampling location and host rejection behavior, genetic differentiation among host species and sampling locations were assessed using AMOVA (Excoffier et al., 1992).

III. RESULTS

A. HOST USE BY SHINY COWBIRDS AT POPULATION LEVEL

Data used for all the analyses described in this section are presented in Appendix I.

At the four study sites, shiny cowbirds parasitized at high frequencies ($\geq 50\%$); only a small proportion of the available hosts (range 5–33%) and either did not use or only used at very low frequencies ($< 25\%$) a large proportion of the available hosts (range 57–92%, Table I).

We tested if shiny cowbirds showed preferences for hosts smaller or larger than themselves by analyzing the association between frequency of parasitism and volume of hosts' eggs. We observed a weak tendency toward a positive association between frequency of parasitism and egg volume in two sites (Santa Fe: Spearman rank correlation: $\rho = 0.29$, $z = 1.84$, $P = 0.07$, $n = 41$

TABLE I

PERCENTAGE OF SPECIES PREVIOUSLY REPORTED AS HOSTS THAT WERE PARASITIZED AT FREQUENCIES EQUAL TO OR HIGHER THAN 50% (≥ 50), BETWEEN 25% AND 50% (≥ 25–<50), BETWEEN 0% AND 25% (>0 AND <25) AND NOT PARASITIZED ($=0$) AT FOUR SITES IN ARGENTINA: BUENOS AIRES ($n = 21$), SANTA FE ($n = 41$), CÓRDOBA ($n = 19$), AND FORMOSA ($n = 51$)

	Frequency of parasitism			
Place	≥ 50	≥ 25–<50	>0–<25	$=0$
Buenos Aires	33(7)	10(2)	33(7)	24(5)
Santa Fe	5(2)	24(10)	39(16)	32(13)
Córdoba	11(2)	16(3)	32(6)	42(8)
Formosa	6(3)	2(1)	18(9)	75(39)

Numbers between parentheses indicate number of host species at each category of frequency of parasitism.

hosts; and Formosa: $\rho = 0.25$, $z = 1.77$, $P = 0.08$, $n = 51$ hosts; Fig. 1), but there was no association between these variables at the other two sites (Buenos Aires: $\rho = 0.24$, $z = 1.06$, $P = 0.29$, $n = 21$ hosts; and Córdoba: $\rho = 0.18$, $z = 0.76$, $P = 0.45$, $n = 19$ hosts; Fig. 1). Within those hosts parasitized at frequencies $\geq 50\%$, some species were smaller and others were larger than the parasite (four smaller and three larger in Buenos Aires; one smaller and two larger in Formosa; and one smaller and one larger in Córdoba, Appendix I).

As to shiny cowbird preferences for the type of nest used by hosts, we observed a preference for open nests in two sites (Buenos Aires: Mann–Whitney *U*-test; $z = -2.00$, $P = 0.05$; and Córdoba: $z = -2.59$, $P = 0.01$; Fig. 2), but there were no preferences in the other two sites (Santa Fe: $z = -0.79$, $P = 0.43$; and Formosa: $z = -0.24$, $P = 0.81$; Fig. 2).

We also tested if shiny cowbirds preferred to parasitize hosts that were more phylogenetically related by analyzing the association between frequency of parasitism and genetic distance between the host and the parasite. We observed a negative association in one site (Santa Fe: Spearman rank correlation; $\rho = -0.43$, $z = 2.34$, $P = 0.02$, $n = 31$ hosts) and a tendency toward a negative association in another site (Córdoba: $\rho = -0.46$, $z = 1.78$, $P = 0.07$, $n = 16$ hosts), but there was no association in the other two sites (Buenos Aires: $\rho = -0.32$, $z = 1.24$, $P = 0.22$, $n = 16$ hosts; and Formosa: $\rho = 0.06$, $z = 0.34$, $P = 0.74$, $n = 35$ hosts; Fig. 3).

Finally, to test if shiny cowbirds showed consistent preferences for some host species, we compared the frequency of parasitism of the same host in different sites. Because the communities of shiny cowbird hosts differed considerably between the more distant sites (Buenos Aires and Formosa), we only performed the comparisons between Buenos Aires and Santa Fe,

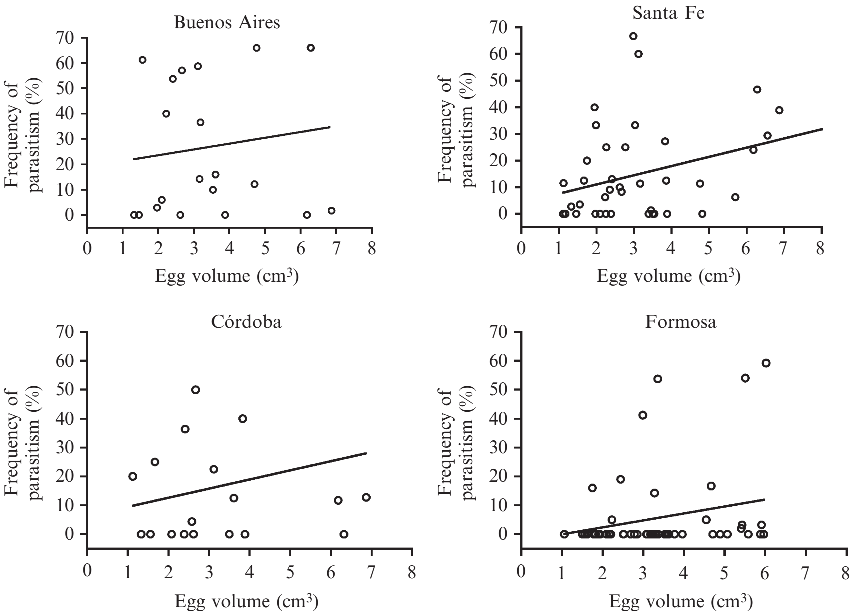

FIG. 1. Relationship between frequency of parasitism and volume of host eggs (as surrogate of host body mass) for shiny cowbird hosts at four sites in Argentina: (A) Buenos Aires ($n = 21$), (B) Santa Fe ($n = 41$), (C) Córdoba ($n = 19$), and (D) Formosa ($n = 51$). There was a nonsignificant tendency toward a positive association in Santa Fe ($P = 0.07$) and Formosa ($P = 0.08$), but no significant association in Buenos Aires ($P = 0.29$) and Córdoba ($P = 0.45$).

which share 15 hosts, and between Santa Fe and Formosa, which share 24 hosts. If shiny cowbirds had consistent preferences for the same host species, we expected a positive association between the frequencies of parasitism of these hosts in different sites. We observed a positive association between frequency of parasitism of same hosts in different sites between Santa Fe and Formosa (Spearman rank correlation; $\rho = 0.48$, $z = 2.31$, $P = 0.02$, $n = 24$ hosts), but there was no association between Buenos Aires and Santa Fe ($\rho = 0.40$, $z = 1.51$, $P = 0.13$, $n = 15$ hosts; Fig. 4).

B. HOST USE BY SCREAMING COWBIRDS AT POPULATION LEVEL

1. *Host Use by Screaming Cowbirds*

The frequency of screaming cowbird parasitism differed among host populations. Baywings were parasitized at a higher frequency in Buenos Aires than in Formosa, and both populations were more frequently

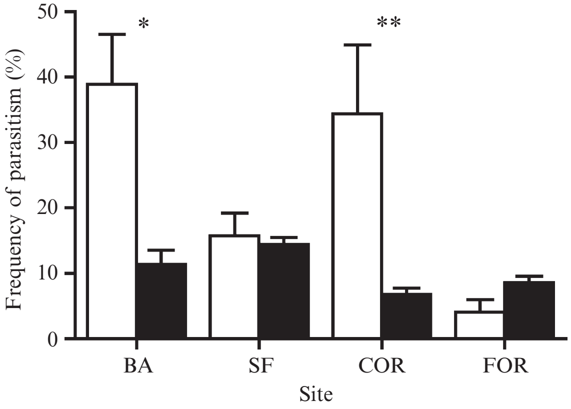

FIG. 2. Frequency of parasitism in hosts of shiny cowbirds with open (white bars) or closed (black bars) nests at four sites in Argentina: (A) Buenos Aires (open: $n = 12$, closed: $n = 9$), (B) Santa Fe (open: $n = 23$, closed: $n = 18$), (C) Córdoba (open: $n = 7$, closed: $n = 12$), and (D) Formosa (open: $n = 32$, closed: $n = 19$). Parasitism was higher in open than in closed nests in Buenos Aires ($P = 0.05$) and Córdoba ($P = 0.01$), but there were no significant differences in Santa Fe ($P = 0.43$) and Formosa ($P = 0.81$).

parasitized than were chopi blackbirds and brown-and-yellow marshbirds (Chi-square test: $\chi_3{}^2 = 392.4$, $P < 0.0001$; Table II). Similarly, the intensity of parasitism differed among host populations (Kruskal–Wallis test: $H_2 = 49.7$, $P < 0.0001$; Table II). Baywings in Buenos Aires were more parasitized than baywings and chopi blackbirds in Formosa (*post hoc* comparisons $P < 0.05$). Multiple parasitism was the prevalent trend in Buenos Aires (93% of parasitized baywing nests had more than one screaming cowbird egg) and Formosa (62% of parasitized baywing nests and 76% of parasitized chopi blackbird nests had more than one screaming cowbird egg). In contrast, only 23% of the parasitized brown-and-yellow marshbird nests were multiply parasitized ($n = 43$ nests; Mermoz and Fernández, 2003).

Screaming cowbirds overlapped in host use with shiny cowbirds when parasitizing baywings and brown-and-yellow marshbirds. There was no association between shiny and screaming cowbird parasitism in baywing nests in Buenos Aires (155/193 nests parasitized by screaming cowbirds only, 1/193 nests parasitized by shiny cowbirds only, and 25/193 nests parasitized by screaming and shiny cowbirds; Chi-square test: $\chi_1{}^2 = 0.01$, $P = 0.91$). In brown-and-yellow marshbird nests, however, screaming and shiny cowbirds tended to overlap in nest use less than expected by chance (193/382 nests parasitized by shiny cowbirds only, 12/382 nests parasitized by screaming cowbirds only, and 31/382 nests parasitized by screaming and shiny cowbirds; Chi-square test: $\chi_1{}^2 = 3.6$, $P = 0.06$).

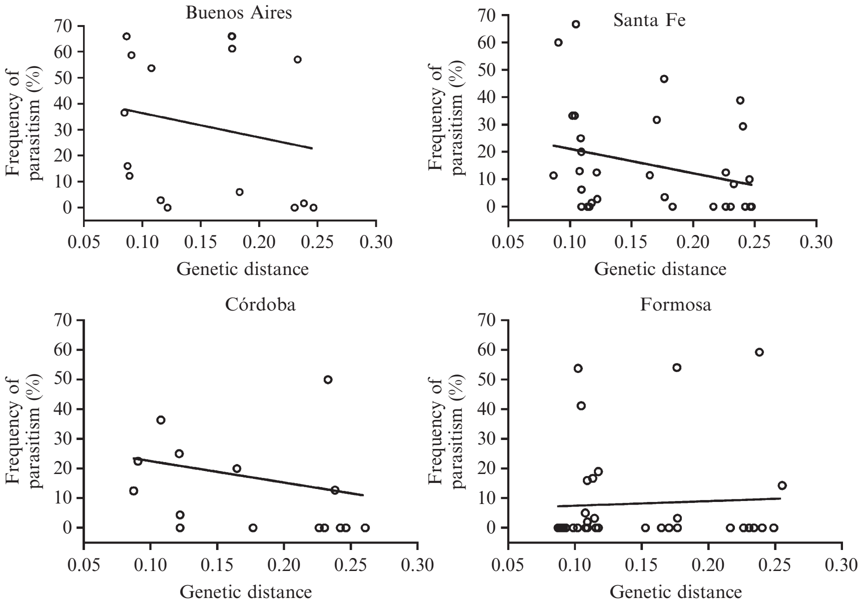

FIG. 3. Relationship between frequency of parasitism and genetic distance between host and parasite for hosts of shiny cowbirds at four sites in Argentina: (A) Buenos Aires ($n = 16$), (B) Santa Fe ($n = 31$), (C) Córdoba ($n = 16$), and (D) Formosa ($n = 35$). There was a significant negative association at Santa Fe ($P = 0.02$), a nonsignificant tendency toward a negative association in Córdoba ($P = 0.07$), but there was no significant association in Buenos Aires ($P = 0.22$) and Formosa ($P = 0.74$).

Despite the small overlap in host use, the chicks of screaming and shiny cowbirds rarely grew alongside each other because most nests with mixed parasitism were depredated. Nevertheless, in baywing nests artificially parasitized with shiny cowbird eggs, the presence of shiny cowbird chicks did not affect the success of screaming cowbird ones. Screaming cowbird chicks fledged in 5/5 nests and 14/15 nests with and without shiny cowbird chicks, respectively (Fisher's Exact test: $P > 0.99$). Although sample sizes are small, data indicate that the presence of screaming cowbird chicks did not affect the survival of shiny cowbird chicks (4/4 and 2/2 shiny cowbirds fledged in nests with and without screaming cowbird chicks, respectively).

2. *Success of Screaming Cowbird Eggs and Chicks in Primary and Alternative Hosts*

There were no differences among host populations in screaming cowbird's hatching success (Kruskal–Wallis test: $H_2 = 2.6$, $P = 0.28$) or chick survival ($H_2 = 0.9$, $P = 0.63$; Fig. 5), but nest survival differed among host

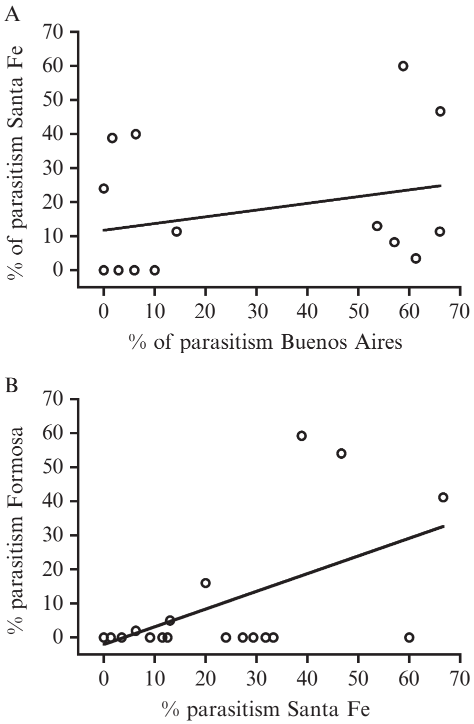

FIG. 4. Relationship between frequencies of parasitism of the same hosts at different sites. (A) Buenos Aires versus Santa Fe ($n = 15$ hosts), (B) Santa Fe versus Formosa ($n = 24$ hosts). There was a positive association of the frequencies of parasitism of the same hosts between Santa Fe and Formosa ($P = 0.02$), but not between Buenos Aires and Santa Fe ($P = 0.13$).

populations (Chi-square test: $\chi_2^2 = 26.4$, $P < 0.0001$; Fig. 5). Nest failure was a major cause of losses of screaming cowbird eggs. About 88% (565/644) of the screaming cowbird eggs laid in baywing nests in Buenos Aires ($n = 126$ nests), 45% (54/121) of those laid in baywing nests in Formosa ($n = 33$ nests), and 52% (182/350) of those laid in chopi blackbird nests ($n = 115$ nests) were lost as a result of nest desertion or predation.

3. *Screaming Cowbird's Reproductive Success in Potentially Suitable Hosts*

Between 2003 and 2006, we artificially parasitized 54 nests of chalk-browed mockingbirds and 33 nests of house wrens with screaming cowbird eggs or newly hatched chicks (De Mársico and Reboreda, 2008b). Only three of 12 (25%) screaming cowbird chicks fledged in successful mockingbird nests ($n = 12$ nests; host brood size: 3.1 ± 0.4, range: 1–5 chicks).

TABLE II

Frequency and Intensity of Parasitism by Screaming Cowbirds of Baywings (at Buenos Aires and Formosa), Chopi Blackbirds, and Brown-and-Yellow Marshbirds

Host	Site	Frequency of parasitism	Intensity of parasitism
Baywing	Buenos Aires	93 (180/193)	4.8 ± 0.2 (168)
Baywing	Formosa	80 (55/69)	2.4 ± 0.2 (50)
Chopi blackbird	Formosa	47 (126/267)	3.0 ± 0.2 (116)
Brown-and-yellow marshbird	Buenos Aires	11 (43/382)	1.3 ± 0.1 (43)

Numbers between parentheses indicate number of nests. Intensity of parasitism was calculated from nests found before or during hosts' laying. Data for parasitism of brown-and-yellow marshbird are from Mermoz and Fernández (2003).

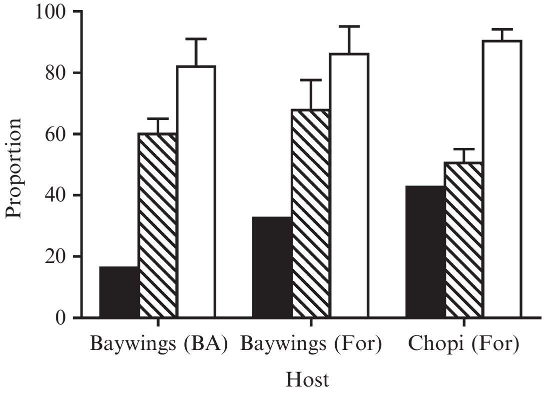

Fig. 5. Black bars indicate the proportion of successful nests (nests that fledged chicks) for two hosts of screaming cowbirds: baywings (*Agelaioides badius*) in Buenos Aires (BA) and Formosa (For), and Formosa, and chopi blackbirds (*Gnorimopsar chopi*) in Formosa. Striped bars indicate hatching success of screaming cowbird eggs (proportion of eggs that hatched), whereas white bars indicate survival of screaming cowbird chicks (proportion of chicks that fledged) in nests of baywings and chopi blackbirds. There were no significant differences in hatching success or chick survival between hosts and sites, but nesting success differed between sites.

The other nine chicks died as a result of competition for food with their nestmates. Screaming cowbird chicks that survived had one or two host nestmates. Survival of screaming cowbird chicks was lower than that reported for shiny cowbird chicks reared by mockingbirds in the same study area and under similar experimental conditions (12/17 chicks fledged, host brood size: 2.4 ± 0.2 chicks, range: 2–4; Fiorini et al., 2009; Fisher's Exact test: $P = 0.03$). In artificially parasitized wren nests, six of 11 (55%)

screaming cowbird chicks fledged successfully (host brood size: 3.0 ± 0.5, range: 1–5, $n = 11$ nests). The remaining chicks died due to heavy infestations with botfly larvae (*Philornis seguyi*). Again, survival of screaming cowbird chicks was lower than that reported for shiny cowbird chicks in wren nests in the same area (23/23, host brood size: 2.7 ± 0.2 chicks, range: 3–5; Fiorini et al., 2009; Fisher's Exact test: $P = 0.002$).

C. Host Use by Shiny and Screaming Cowbirds at Individual Level

Haplotype frequency distributions among hosts revealed nonrandom laying in both cowbird species. In shiny cowbirds, we found differences in the distribution of haplotypes between house wrens and the other three hosts (rufous-collared sparrows, brown-and-yellow marshbirds, and chalk-browed mockingbirds; pairwise Φ_{ST} values = 0.20–0.23, $P < 0.001$). Similarly, in the screaming cowbird, we found differences in the distribution of haplotypes between baywings and chopi blackbirds ($\Phi_{ST} = 0.05$, $P = 0.04$). In a scenario of random laying, we would expect to find haplotypes equally distributed among hosts. Similarly, if females are host specialists at individual level but do not share host use with their mothers, haplotype distribution should be randomly distributed. This would arise from females sharing the haplotype with their mothers but using a different host. Hence, the same haplotype would be represented in all hosts. If this happened in all females, haplotypes would be equally found in all hosts. Figure 6 shows haplotype frequencies for one host species of shiny and screaming cowbirds compared

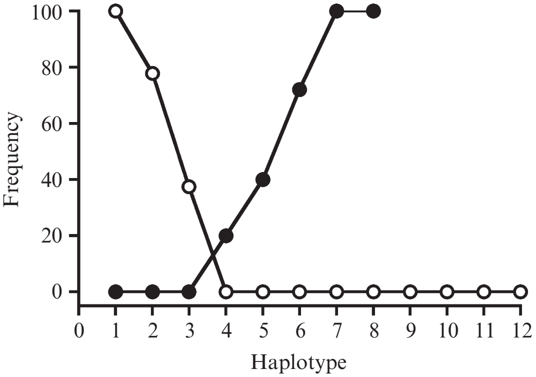

Fig. 6. Haplotype (H1–H12) frequency for one shiny cowbird (open symbols) and one screaming cowbird (closed symbols) host compared with another host of the study area. Shiny cowbird: house wren (vs. chalk-browed mockingbird); screaming cowbird: chopi blackbird (vs. baywing). Data taken from Mahler et al. (2007, 2009), haplotype numeration is arbitrary.

with another host of the study area. Random host use would yield frequencies close to 50% for all haplotypes, while nonrandom host use shows some haplotypes only (or found in one host (100%) or in the other one (0%)).

IV. Discussion

A. Host Use by Shiny Cowbirds at Population Level

Our results show that shiny cowbirds are much less generalists at population level than previously assumed, as they did not parasitize most available hosts and parasitized at high frequencies only a few of them. In three of the four analyzed sites, only two to three hosts were parasitized at high frequencies ($\geq 50\%$) and in these sites shiny cowbirds did not use up to 75% of the available hosts. These results contrast with the general view of shiny cowbirds as extreme generalists, and indicate that host use by shiny cowbirds at a community level is restricted to a few preferred species.

Regarding the characteristics of these preferred species, we did not find clear evidences of shiny cowbird's preferences for hosts larger or smaller than themselves. In two sites (Santa Fe and Formosa), we observed a nonsignificant trend toward a preference for hosts larger than the parasite, but in the other two sites there was no association between frequency of parasitism and hosts' body mass. Similarly, the category of hosts used at high frequencies ($\geq 50\%$) included hosts both larger and smaller than the parasite in three of the four sites. Mason (1986) proposed that shiny cowbirds prefer large hosts because they provide higher reproductive success for the parasite. However, data on reproductive success of shiny cowbirds in hosts that differ considerably in body size indicate that there is no clear association between reproductive success and host body mass (Fiorini et al., 2005), and that other hosts' life history traits, such as diet (Lichtenstein, 1998), length of the incubation period (Mermoz and Reboreda, 2003), or frequency of brood reduction (Astié and Reboreda, 2009), can better predict the success of shiny cowbirds in a particular host.

We found some evidences of shiny cowbird's preferences for using hosts that build open nests in two of the sites (Buenos Aires and Córdoba). However, in the other two sites, open and closed nesters were parasitized at similar frequencies indicating that there is no general preference for hosts with open or closed nests. The differences observed between sites are better explained by the inclusion or not of some host species at different sites. In particular, shiny cowbirds parasitize at high frequencies the closed nester rufous hornero (*F. rufus*) in Formosa and Santa Fe, but not in Buenos Aires and Córdoba. This host ejects shiny cowbird eggs narrower than their own using the width of the egg as a cue (Mason and Rothstein, 1986). Rufous horneros have considerably larger body mass (and therefore wider eggs) than shiny cowbirds in Buenos Aires and Córdoba, and therefore at these sites they are able to discriminate between their own and shiny cowbird eggs. On the contrary, in Formosa, rufous horneros are 25% smaller in body mass than in Buenos Aires and lay eggs similar in width to those of shiny cowbirds, making egg ejection more difficult (Di Giacomo, 2005).

There were no clear evidences of shiny cowbird's preferences for using host species that were phylogenetically more related. We observed a negative association in one site (Santa Fe), and a tendency toward a negative association in another site (Córdoba), but there was no association in the other two sites. The most parsimonious explanation for these results is that the frequent use of hosts of more related families (i.e., Icteridae and Emberizidae) in some sites resulted in a negative association between genetic distance and frequency of parasitism, whereas the use of hosts of less related families (i.e., Tyrannidae, Furnariiidae) in other sites resulted in no association.

Ortega (1998) reviewed host use by shiny cowbirds in different areas of its distribution and noted that most parasitized hosts differed markedly between areas. This author concluded that these differences may reflect alternatives in the host community. Our results are partly consistent with Ortega's interpretation, as some of the differences in host use between sites can be attributed to differences in the host community (i.e., highly parasitized hosts that were frequent in one site and absent or present at low density in the other site). When we compared the frequencies of parasitism between host species that were present in two sites, we observed that in some cases, shiny cowbirds parasitized the same species at similar frequencies in both sites, showing consistent host use across areas. However, other host species were not consistently used between sites, indicating that preferences for some species may vary regionally depending on the alternative hosts present in the community. These changes in host use suggest that where hosts of ''high quality'' are at low density or absent, shiny cowbirds can use hosts of low quality (e.g., Astié and Reboreda, 2009).

B. Host Use by Screaming Cowbirds at Population Level

The incidence of screaming cowbird parasitism varied among and within host species. Baywing was the main host with frequencies of parasitism that largely exceeded those observed in chopi blackbirds (this study) and brown-and-yellow marshbirds (Mermoz and Fernández, 2003). However, screaming cowbird parasitism was not homogeneous across baywings' distribution, as in Buenos Aires the frequency and intensity of parasitism were higher than in Formosa. This regional variation in the incidence of parasitism may indicate that the number of nests available for parasitism could be more limited in Buenos Aires, resulting in more screaming cowbird females overlapping in host use or parasitizing a single nest more than once. However, we cannot disentangle the causes of this variation because several biotic and abiotic factors are likely to interact in determining the frequency of parasitism at any given locality. The differences in frequency of parasitism among host species are even more striking, since screaming cowbird eggs and chicks appear to be equally successful in nests of the three hosts. The results presented here are consistent with the idea that screaming cowbirds exhibit a rooted preference for baywings and would have secondarily colonized the other host species.

Other highly specialized avian brood parasites have been able to colonize new species apart from its main host. In the host-specific parasitic indigobirds (*Vidua* spp.), misimprinting or egg-laying mistakes presumably caused host shifts that led to new host–parasite associations and sympatric speciation in the parasites (Payne et al., 2000; Sorenson et al., 2003). In some cuckoo species, flexibility in host preference, or a combination of host and habitat preferences, allows parasites to use secondary hosts if the primary one is spatially or temporally unavailable (Langmore and Kilner, 2007). The observed pattern of host use in screaming cowbirds is compatible with the occurrence of egg-laying mistakes or with some flexibility in host use at individual level, but the latter hypothesis is not supported by the frequency distribution of mtDNA haplotypes among hosts (Mahler et al., 2009).

Interestingly, the screaming cowbird overlapped little in host use with its generalist relative, the shiny cowbird. Both cowbird species occasionally converged in nests of baywings and brown-and-yellow marshbirds, but they used these hosts at very different frequencies, as has been previously reported (Fraga, 1998; Mason, 1980; Mermoz and Fernández, 2003). Similar patterns of host use were observed in other obligate brood parasites that live in sympatry (Brooker and Brooker, 1990; Ellison et al., 2006). For instance, the brown-headed cowbird is sympatric with the bronzed cowbird in southern North America, but they barely overlap in host use (Chace, 2005; Ellison et al., 2006). Furthermore, like screaming and shiny cowbirds, brown-headed and bronzed cowbirds exhibit preferences for certain host species, which were often multiply parasitized despite the availability of unparasitized nests of other suitable host species (Ellison et al., 2006). For some Australian cuckoo species (*Chrysococcys* spp.) that partially overlap in the use of secondary hosts, it has been suggested that the selective destruction of heterospecific parasitic eggs by cuckoo females may have led to host specialization (Brooker and Brooker, 1990). Likewise, shiny cowbirds often puncture eggs when visiting nests (Astié and Reboreda, 2006; Fiorini et al., 2009; Massoni and Reboreda, 1998), thus the risk of egg losses may preclude screaming cowbird females from using hosts regularly parasitized by shiny cowbirds. However, experiments involving the cross-fostering of screaming cowbird eggs to nests of shiny cowbird's primary hosts provided little support for this idea, as cross-fostered eggs had similar survival rates compared with those laid in baywing nests (De Mársico and Reboreda, 2008b). Nonetheless, available data are insufficient to assess the role of interspecific competition in driving host specialization in screaming cowbirds. In particular, we still lack studies that test the outcome of interspecific competition between cowbird chicks when reared in the same nest, and further experimental work is needed to determine whether the occurrence of screaming and shiny cowbird chicks in the same nest affect each other's growth rate and survival. Our results suggest that cowbird chicks did not suffer higher mortality rates when reared together in baywing nests, but brood reduction is in itself rare in this host species (De Mársico et al., 2010; Fraga, 1998). It would be interesting to test the effect of the presence of shiny cowbird chicks on the survival of screaming cowbird chicks, and vice versa, in hosts that impose higher levels of competition to parasitic chicks, for example, host species that do not breed cooperatively or whose chicks can compete strongly for food with the parasitic young.

We found some support for the hypothesis that host specialization in screaming cowbirds would be favored by a higher reproductive success in its main host compared to other suitable but unused hosts (De Mársico and Reboreda, 2008b). In particular, screaming cowbird chicks suffered higher mortality rates when experimentally cross-fostered to nests of chalk-browed mockingbirds and house wrens than when reared by baywings. In chalk-browed mockingbird nests, larger host chicks often outcompeted screaming cowbird chicks, despite the fact that the latter were always the first to hatch. Larger host species often impose severe costs to parasitic chicks, especially when the host's incubation period is similar to that of the parasite (Fiorini et al., 2009; Lichtenstein, 1998; Scott and Lemon, 1996). Screaming cowbird chicks suffered higher mortality rates than shiny cowbird chicks in chalk-browed mockingbirds in the same study area and reared in similar conditions (Fiorini et al., 2009). These preliminary results would indicate that screaming and shiny cowbird chicks may actually differ in their competitive abilities, and provide indirect evidence supporting that interspecific competition within the brood may be a major selective force underlying host selection in screaming cowbirds.

Our results are consistent with the hypothesis of a strong host preference in screaming cowbirds. Preferences for a nest or habitat type are unlikely because baywings breed in a wide variety of closed nests (including cavities) and share their habitat with many other passerines that can be suitable hosts. Screaming cowbirds have a prolonged association with adult and juvenile baywings after leaving the nest (Fraga, 1998), and adults of both species often forage in mixed flocks throughout the year and share roosting sites, thus providing screaming cowbirds with broad opportunities to imprint on the primary host. Further studies are necessary to disentangle the cues and mechanisms involved in host choice and maintenance of host preferences in this brood parasite.

C. Host Use by Shiny and Screaming Cowbirds at Individual Level

Haplotype frequency distribution showed a nonrandom laying pattern in females of both shiny and screaming cowbirds. Although laying strategies are very different at population level in both species, with shiny cowbirds being extreme generalists and screaming cowbirds using mainly one host along its distribution, host use at individual level seems to be based on certain preferences in both species. In the shiny cowbird, females that parasitized house wrens differed genetically from those parasitizing the other three hosts. Similarly, in the screaming cowbird there was a genetic differentiation between females that parasitized baywings and chopi blackbirds.

Selection for particular hosts is widespread among obligate brood parasites (Cherry and Bennett, 2001; Gibbs et al., 2000; Starling et al., 2006). In species that are host specialists, individuals recognize their host and always lay eggs in their nests (Sorenson et al., 2003). In some brood parasites, recognition of the host is based on an imprinting process with the foster parents (Payne et al., 2002), and misimprinting may lead to host switches (Sorenson et al., 2003). This has been documented in African *Vidua* finches where speciation parallels host use. But host specificity has also been found in individuals of host-generalist brood parasites. In several cuckoo species, constant host use has led to host-specific lineages, which evolved egg mimicry to deceive hosts and avoid the rejection of their eggs (Cherry and Bennett, 2001; Moksnes and Røskraft, 1995; Starling et al., 2006). In American cowbirds, in contrast, individual host-specificity does not seem to be so strict. Direct evidences have shown that in brown-headed and bronzed cowbirds, populations are composed of both specialist and generalist females (Ellison et al., 2006). However, generalist females only used some of the available hosts in the area, indicating that this generalist behavior is not following a shotgun strategy by which females lay in all available nests, but that it is somehow restricted to some host species. We have found a similar pattern in shiny cowbirds. Different populations are selectively parasitizing distinct avian communities where preferred hosts vary. Moreover, we found indirect evidence supporting host preferences at individual level in Buenos Aires Province. While some females preferentially parasitized house wrens, others preferentially parasitized three other species (Mahler et al., 2007). A common denominator of these three species was nest type, since all of them build open-cup nests, contrary to house wrens that build their nests in cavities. Hence, laying preference may not be related to a particular host species in this parasitic cowbird but to a certain type of nest. Whether this group of females is composed of both generalists and specialists has to be determined by direct evidence. We have also found indirect evidence for nonrandom laying in the screaming cowbird. In an area where two host species coexist, some females preferred to lay in nests of baywings and others in nests of chopi blackbirds. However, in the majority of its distribution, screaming cowbirds only parasitize baywings.

D. Host Imprinting, Recognition Errors, and Colonization of New Hosts

Why is host use differently constrained in cowbird species? One possibility is that imprinting to particular hosts is disparately strong and ‘‘mistakes’’ in host recognition occur in distinct frequencies in host-specialist and host-generalist brood parasites (Ellison et al., 2006). Albeit host use is restricted at individual level in all species, the number of hosts used by a population might vary among cowbird species. So, individual screaming cowbirds use baywings in most of its distribution, but in some areas some females use alternative hosts, like the chopi blackbird or the brown-and-yellow marshbird. It is possible that in these areas the ‘‘colonization’’ of a new host occurred due to recognition errors when parasitic females looked for host nests (i.e., they laid eggs in nests of a host other than the foster parent). If this new host successfully reared parasitic females, these females would afterward look for this host for laying. Examples of this type of recognition error have been reported recently for screaming cowbirds, which parasitized nests of two new hosts that were close to nests of hosts commonly used by this parasite (Di Giacomo et al., 2010).

Another potential source of ‘‘mistakes’’ that may result in the colonization of new hosts by brood parasites is to copy the behavior of other females when searching for host nests. If a parasitic female was not successful during the previous day in finding a suitable nest to parasitize, she may follow conspecific females the next day and thus she may increase the probability of successful parasitism. This process of social learning (i.e., the acquisition of behavior influenced by the observation of, or the interaction with, another animal) is especially beneficial to animals that live in groups, like birds that feed or roost in flocks (Galef and Giraldeau, 2001). Shiny and screaming cowbirds roost communally at night in large numbers (Cruz et al., 1990; Ortega, 1998). These species parasitize hosts at dawn and it is relatively common that several conspecific females visit the same nest together

(De Mársico and Reboreda, 2008a; Ros Gloag, personal communication). These observations suggest that in addition to finding nests individually, some females could find host nests by social learning.

Host imprinting may also explain host use at population level, where different shiny cowbird populations use different hosts. According to this interpretation, females using a particular host or hosts colonized new areas and then new hosts were acquired through mistakes that occurred in nests of available species. Because mistakes occurring at different sites are unlikely to be similar, differences in host use among sites can be expected.

If host imprinting is the general mechanism to explain host learning, and ‘‘mistakes’’ in host recognition may allow parasites to colonize new hosts, how can we explain the striking differences in host use by specialist and generalist brood parasites? One possible explanation for these differences is that in specialist brood parasites, like the screaming cowbird, the requirements of eggs and chicks to be successful in new hosts are quite restricted. This may have led to negative selective pressures on females that make mistakes, which favored strong host imprinting. On the contrary, in generalist brood parasites like the shiny cowbird, mistakes of females when searching for nests of the host where they were reared may be advantageous, as their eggs and chicks can be successfully incubated and reared in a wide range of hosts. This may have led to positive selective pressures on females that make mistakes, which resulted in weaker host imprinting. This putative variation in the strength of host imprinting can also explain differences within generalist brood parasites, like the brown-headed cowbird, in which at individual level some females are specialists and others generalists (e.g., Alderson et al., 1999; Strausberger and Ashley, 2005; Woolfenden et al., 2003).

V. Conclusions

The data presented in this study indicate that parasitism by the host-generalist shiny cowbird does not occur at random at both population and individual levels. At population level, parasitism was strongly biased to a few host species within each avian community, indicating that shiny cowbird females are much less generalist than previously thought. At individual level, evidences for a genetic differentiation between shiny cowbird females that parasitize different hosts provide further support for a nonrandom laying behavior. Similarly, host use by screaming cowbirds at population level reflects a strong preference for baywings, although parasite's reproductive success was similar in the secondary hosts. Genetic differentiation between females that parasitize baywings and chopi blackbirds also provides indirect evidence of a nonrandom laying behavior by screaming cowbird females and suggests that they may have secondarily colonized the alternative hosts.

One explanation for the observed preferences of host use in both species is that parasitic females imprint on some host characteristics and when adults, they use these cues to locate and parasitize hosts' nests. From this perspective, changes in host use or colonization of new hosts would be the consequence of recognition errors, which result in parasitic females laying eggs in nests of hosts different from the foster parents. However, for a parasite to colonize a new host species, it is also necessary that the new host successfully rears parasitic females. Our results provide some evidence that the success of screaming cowbird's chicks differs between baywing and other suitable but unused hosts. This differential success may explain why host switches are infrequent in this species. In contrast, shiny cowbird chicks seem to be able to successfully exploit a wide range of host species, which could make recognition errors less costly, or even advantageous, for parasitic females of this species.

To know how a brood parasite uses hosts at population and individual levels is critical for better understanding of parasites' population dynamics. Future areas of research that would greatly contribute to increase our knowledge of host use by shiny and screaming cowbirds would be to assess the importance of host imprinting and social learning in the acquisition of host preferences by individual females, to obtain direct evidence of the pattern of host use at individual level, and to assess whether the pattern of host use at population level is related to differences between screaming and shiny cowbird chicks in their ability to face competition for food within the brood.

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APPENDIX I

List of shiny cowbird's hosts analyzed at the four study sites (Buenos Aires, Córdoba, Santa Fe, and Formosa). For each host/site, we indicate the number of nests observed, frequency of parasitism, volume of host's eggs (estimated according to Hoyt, 1979), if the nest is open or closed (c and d indicate cavity or domed nests) and the genetic distance between the host and the parasite (estimated with Phylip v.3.68 Package, Felsenstein, 2008). The last column indicates the source of the data

Site	Family	Host	# Nests	Parasitism	Egg volume	Nest type	Genetic distance	Reference
Buenos Aires	Mimidae	*Mimus saturninus*	165	66	6.28	Open	0.177	Fiorini and Reboreda (2006)
Buenos Aires	Icteridae	*Pseudoleistes virescens*	418	66	4.76	Open	0.087	Mermoz and Reboreda (2003)
Buenos Aires	Turdidae	*Turdus rufiventris*	41	66	6.29	Open	0.177	Sackmann and Reboreda (2003)
Buenos Aires	Troglodytidae	*Troglodytes aedon*	75	61	1.56	Closed (c)	0.177	Tuero et al. (2007)
Buenos Aires	Icteridae	*Agelaius ruficapillus*	77	47	3.12	Open	0.091	Lyon (1997)
Buenos Aires	Tyrannidae	*Tyrannus savanna*	7	57	2.67	Open	0.233	Mason (1986)
Buenos Aires	Emberizidae	*Zonotrichia capensis*	41	54	2.41	Open	0.108	Fernández and Duré Ruiz (2007)
Buenos Aires	Tyrannidae	*Satrapa icterophys*	10	40	2.23	Open	–	Mason (1986)
Buenos Aires	Icteridae	*Agelaius thilius*	213	37	3.19	Open	0.085	Massoni and Reboreda (1998)
Buenos Aires	Icteridae	*Agelaioides badius*	193	16	3.61	Closed (c, d)	0.088	De Mársico et al. (2010)
Buenos Aires	Furnariidae	*Phacellodomus striaticollis*	7	14	3.16	Closed (d)	–	Mason (1986)
Buenos Aires	Icteridae	*Amblyramphus holosericeus*	49	12	4.71	Open	0.089	Fernandez and Mermoz (2000)
Buenos Aires	Icteridae	*Sturnella superciliaris*	10	10	3.54	Open	–	Tuero (personal communication)
Buenos Aires	Hirundinidae	*Tachycineta leucorrhoa*	50	6	2.10	Closed (c)	0.183	Massoni et al. (2006)

Buenos Aires	Emberizidae	*Sicalis flaveola*	35	3	1.97	Closed (c)	0.116	Mason (1986)
Buenos Aires	Furnariidae	*Furnarius rufus*	59	2	6.87	Closed (d)	0.238	Massoni and Reboreda (unpubished data)
Buenos Aires	Furnariidae	*Anumbius annumbi*	11	0	3.88	Closed (d)	0.246	Mason (1986)
Buenos Aires	Fringillidae	*Carduelis magellanica*	7	0	1.32	Open	0.122	Mason (1986)
Buenos Aires	Furnariidae	*Phleocryptes melanops*	22	0	2.62	Closed (d)	0.230	Mason (1986)
Buenos Aires	Tyrannidae	*Pitangus sulphuratus*	7	0	6.18	Closed (d)	–	Mason (1986)
Buenos Aires	Tyrannidae	*Pyrocephalus rubinus*	22	0	1.46	Open	–	Mason (1986)
Cordoba	Mimidae	*Mimus saturninus*	46	87	6.28	Open	0.177	Salvador (1983)
Cordoba	Tyrannidae	*Tyrannus savanna*	24	50	2.67	Open	0.233	Salvador (1983)
Cordoba	Tyrannidae	*Machetornis risosa*	5	40	3.83	Closed (c)	–	Salvador (1983)
Cordoba	Emberizidae	*Zonotrichia capensis*	22	36	2.41	Open	0.108	Salvador (1983)
Cordoba	Emberizidae	*Sicalis luteola*	16	25	1.67	Open	0.122	Salvador (1983)
Cordoba	Icteridae	*Agelaius ruficapillus*	213	23	3.12	Open	0.091	Salvador (1983)
Cordoba	Polioptilidae	*Polioptila dumicola*	5	20	1.12	Open	0.165	Salvador (1983)
Cordoba	Furnariidae	*Furnarius rufus*	39	13	6.87	Closed (d)	0.238	Salvador (1983)
Cordoba	Icteridae	*Agelaioides badius*	8	13	3.61	Closed (c,d)	0.088	Salvador (1983)
Cordoba	Tyrannidae	*Pitangus sulphuratus*	17	12	6.18	Closed (d)	–	Salvador (1983)
Cordoba	Ploceidae	*Passer domesticus*	45	4	2.58	Closed (c)	0.122	Salvador (1983)
Cordoba	Furnariidae	*Anumbius annumbi*	12	0	3.88	Closed (d)	0.246	Salvador (1983)
Cordoba	Furnariidae	*Coryphistera alaudina*	16	0	3.50	Closed (d)	0.242	Salvador (1983)
Cordoba	Furnariidae	*Phacellodomus sibilatrix*	15	0	2.39	Closed (d)	0.226	Salvador (1983)
Cordoba	Furnariidae	*Phleocryptes melanops*	14	0	2.62	Closed (d)	0.230	Salvador (1983)
Cordoba	Furnariidae	*Pseudoseisura lophotes*	8	0	6.32	Closed (d)	–	Salvador (1983)
Cordoba	Emberizidae	*Sporophila caerulescens*	16	0	1.33	Open	0.122	Salvador (1983)
Cordoba	Furnariidae	*Synallaxis albescens*	38	0	2.08	Closed (d)	0.261	Salvador (1983)
Cordoba	Troglodytidae	*Troglodytes aedon*	43	0	1.56	Closed (c)	0.177	Salvador (1983)
Santa Fe	Icteridae	*Icterus cayanensis*	6	67	2.98	Closed (d)	0.105	De La Peña (2005)
Santa Fe	Icteridae	*Agelaius ruficapillus*	10	60	3.12	Open	0.091	De La Peña (2005)
Santa Fe	Mimidae	*Mimus saturninus*	60	47	6.28	Open	0.177	De La Peña (2005)
Santa Fe	Tyrannidae	*Fluvicola pica*	35	40	1.95	Closed (d)	–	De La Peña (2005)
Santa Fe	Furnariidae	*Furnarius rufus*	18	39	6.87	Closed (d)	0.238	De La Peña (2005)
Santa Fe	Emberizidae	*Coryphospingus cucullatus*	9	33	1.99	Open	0.102	De La Peña (2005)

(*Continued*)

APPENDIX I (*Continued*)

Site	Family	Host	# Nests	Parasitism	Egg volume	Nest type	Genetic distance	Reference
Santa Fe	Emberizidae	*Saltatricula multicolor*	12	33	3.03	Open	0.104	De La Peña (2005)
Santa Fe	Turdidae	*Turdus amaurochalinus*	22	32	8.44	Open	0.171	De La Peña (2005)
Santa Fe	Thamnophilidae	*Taraba major*	34	29	6.56	Open	0.240	De La Peña (2005)
Santa Fe	Tyrannidae	*Machetornis risosa*	11	27	3.83	Closed (c)	–	De La Peña (2005)
Santa Fe	Tyrannidae	*Pachyramphus polychopterus*	8	25	2.77	Closed (d)	–	De La Peña (2005)
Santa Fe	Emberizidae	*Poospiza nigrorufa*	8	25	2.26	Open	0.109	De La Peña (2005)
Santa Fe	Tyrannidae	*Pitangus sulphuratus*	25	24	6.18	Closed (d)	–	De La Peña (2005)
Santa Fe	Emberizidae	*Poospiza melanoleuca*	20	20	1.75	Open	0.109	De La Peña (2005)
Santa Fe	Emberizidae	*Zonotrichia capensis*	23	13	2.41	Open	0.108	De La Peña (2005)
Santa Fe	Furnariidae	*Phacellodomus ruber*	8	13	3.86	Closed (d)	0.226	De La Peña (2005)
Santa Fe	Emberizidae	*Sicalis luteola*	8	13	1.67	Open	0.122	De La Peña (2005)
Santa Fe	Polioptilidae	*Polioptila dumicola*	96	12	1.12	Open	0.165	De La Peña (2005)
Santa Fe	Furnariidae	*Phacellodomus striaticollis*	35	11	3.16	Closed (d)	–	De La Peña (2005)
Santa Fe	Icteridae	*Pseudoleistes virescens*	35	11	4.76	Open	0.087	De La Peña (2005)
Santa Fe	Furnariidae	*Asthenes baeri*	10	10	2.62	Closed (d)	0.246	De La Peña (2005)
Santa Fe	Tyrannidae	*Griseotyrannus aurantioatrocristatus*	22	9	2.36	Open	–	De La Peña (2005)
Santa Fe	Tyrannidae	*Tyrannus savanna*	12	8	2.67	Open	0.233	De La Peña (2005)
Santa Fe	Cardinalidae	*Saltator coerulescens*	16	6	5.70	Open	0.109	De La Peña (2005)
Santa Fe	Tyrannidae	*Satrapa icterophrys*	48	6	2.23	Open	–	De La Peña (2005)
Santa Fe	Troglodytidae	*Troglodytes aedon*	57	4	1.56	Closed (c)	0.177	De La Peña (2005)
Santa Fe	Emberizidae	*Sporophila caerulescens*	36	3	1.33	Open	0.122	De La Peña (2005)
Santa Fe	Emberizidae	*Paroaria coronata*	73	1	3.45	Open	0.118	De La Peña (2005)
Santa Fe	Furnariidae	*Anumbius annumbi*	13	0	3.88	Closed (d)	0.246	De La Peña (2005)
Santa Fe	Furnariidae	*Certhiaxis cinnamomea*	7	0	2.25	Closed (d)	0.231	De La Peña (2005)
Santa Fe	Furnariidae	*Coryphistera alaudina*	6	0	3.50	Closed (d)	0.242	De La Peña (2005)
Santa Fe	Furnariidae	*Cranioleuca pyrrhophia*	15	0	2.10	Closed (d)	0.216	De La Peña (2005)

Santa Fe	Furnariidae	*Phacellodomus sibilatrix*	16	0	2.39	Closed (d)	0.226	De La Peña (2005)
Santa Fe	Tyrannidae	*Pyrocephalus rubinus*	19	0	1.46	Open	–	De La Peña (2005)
Santa Fe	Cardinalidae	*Saltator aurantiirostris*	8	0	4.82	Open	0.109	De La Peña (2005)
Santa Fe	Tyrannidae	*Serpophaga subcristata*	13	0	1.11	Open	0.248	De La Peña (2005)
Santa Fe	Emberizidae	*Sicalis flaveola*	25	0	1.97	Closed (c)	0.116	De La Peña (2005)
Santa Fe	Icteridae	*Sturnella superciliaris*	9	0	3.54	Open	0.114	De La Peña (2005)
Santa Fe	Hirundinidae	*Tachycineta leucorrhoa*	13	0	2.10	Closed (c)	0.183	De La Peña (2005)
Santa Fe	Tyrannidae	*Xenopsaris albinucha*	16	0	1.17	Open	–	De La Peña (2005)
Santa Fe	Tyrannidae	*Xolmis irupero*	7	0	3.39	Closed (c)	–	De La Peña (2005)
Formosa	Furnariidae	*Furnarius rufus*	59	59	6.02	Closed (d)	0.238	Di Giacomo (2005)
Formosa	Mimidae	*Mimus saturninus*	37	54	5.51	Open	0.177	Di Giacomo (2005)
Formosa	Icteridae	*Cacicus chrysopterus*	117	54	3.36	Closed (d)	0.102	Di Giacomo (2005)
Formosa	Icteridae	*Icterus cayanensis*	17	41	2.99	Closed (d)	0.105	Di Giacomo (2005)
Formosa	Emberizidae	*Paroaria capitata*	21	19	2.44	Open	0.118	Di Giacomo (2005)
Formosa	Emberizidae	*Embernagra platensis*	12	17	4.67	Open	0.113	Di Giacomo (2005)
Formosa	Emberizidae	*Poospiza melanoleuca*	25	16	1.75	Open	0.109	Di Giacomo (2005)
Formosa	Thamnophilidae	*Thamnophilus doliatus*	7	14	3.28	Open	0.255	Di Giacomo (2005)
Formosa	Tyrannidae	*Myiodinastes maculatus*	20	5	4.55	Closed (c)	–	Di Giacomo (2005)
Formosa	Emberizidae	*Zonotrichia capensis*	20	5	2.23	Open	0.108	Di Giacomo (2005)
Formosa	Turdidae	*Turdus rufiventris*	30	3	5.91	Open	0.177	Di Giacomo (2005)
Formosa	Icteridae	*Cacicus solitarius*	31	3	5.43	Closed (d)	0.115	Di Giacomo (2005)
Formosa	Cardinalidae	*Saltator coerulescens*	50	2	5.41	Open	0.109	Di Giacomo (2005)
Formosa	Icteridae	*Agelaioides badius*	70	0	3.56	Closed (c,d)	0.088	Di Giacomo (2005)
Formosa	Icteridae	*Agelaius cyanopus*	60	0	3.23	Open	0.092	Di Giacomo (2005)
Formosa	Icteridae	*Agelaius ruficapillus*	100	0	3.08	Open	0.091	Di Giacomo (2005)
Formosa	Icteridae	*Amblyramphus holosericeus*	15	0	4.71	Open	0.089	Di Giacomo (2005)
Formosa	Emberizidae	*Amnodramus humeralis*	23	0	2.16	Open	–	Di Giacomo (2005)
Formosa	Emberizidae	*Arremon flavirostris*	5	0	3.09	Closed (d)	–	Di Giacomo (2005)
Formosa	Furnariidae	*Certhiaxis cinnamomea*	45	0	2.20	Closed (d)	0.231	Di Giacomo (2005)
Formosa	Emberizidae	*Coryphospingus cucullatus*	18	0	1.90	Open	0.102	Di Giacomo (2005)
Formosa	Furnariidae	*Cranioleuca pyrrhophia*	7	0	1.83	Closed (d)	0.216	Di Giacomo (2005)
Formosa	Cardinalidae	*Cyanocompsa brissonii*	9	0	2.78	Open	0.099	Di Giacomo (2005)

(*Continued*)

APPENDIX I (*Continued*)

Site	Family	Host	# Nests	Parasitism	Egg volume	Nest type	Genetic distance	Reference
Formosa	Vireonidae	*Cyclarhis gujanensis*	5	0	3.53	Open	0.153	Di Giacomo (2005)
Formosa	Emberizidae	*Donacospiza albifrons*	11	0	2.09	Open	–	Di Giacomo (2005)
Formosa	Emberizidae	*Emberizoides herbicola*	30	0	3.25	Open	0.109	Di Giacomo (2005)
Formosa	Tyrannidae	*Empidonomus varius*	8	0	2.69	Open	–	Di Giacomo (2005)
Formosa	Furnariidae	*Furnarius cristatus*	6	0	3.37	Closed (d)	–	Di Giacomo (2005)
Formosa	Icteridae	*Gnorimopsar chopi*	77	0	5.07	Closed (c)	0.093	Di Giacomo (2005)
Formosa	Tyrannidae	*Griseotyrannus aurantioatrocristatus*	23	0	2.52	Open	–	Di Giacomo (2005)
Formosa	Tyrannidae	*Machetornis risosa*	30	0	3.63	Closed (c)	–	Di Giacomo (2005)
Formosa	Emberizidae	*Paroaria coronata*	50	0	3.31	Open	0.118	Di Giacomo (2005)
Formosa	Furnariidae	*Phacellodomus ruber*	30	0	3.96	Closed (d)	0.226	Di Giacomo (2005)
Formosa	Furnariidae	*Phacellodomus sibilatrix*	12	0	2.51	Closed (d)	0.226	Di Giacomo (2005)
Formosa	Tyrannidae	*Pitangus sulphuratus*	120	0	5.88	Closed (d)	–	Di Giacomo (2005)
Formosa	Polioptilidae	*Polioptila dumicola*	40	0	1.06	Open	0.165	Di Giacomo (2005)
Formosa	Hirundinidae	*Progne tapera*	8	0	3.18	Closed (c)	–	Di Giacomo (2005)
Formosa	Tyrannidae	*Pseudocolopteryx sclateri*	30	0	1.06	Open	–	Di Giacomo (2005)
Formosa	Tyrannidae	*Pyrocephalus rubinus*	13	0	1.50	Open	–	Di Giacomo (2005)
Formosa	Cardinalidae	*Saltator aurantiirostris*	10	0	4.89	Open	0.109	Di Giacomo (2005)
Formosa	Emberizidae	*Sicalis flaveola*	5	0	1.94	Closed (c)	0.116	Di Giacomo (2005)
Formosa	Tyrannidae	*Suiriri suiriri*	12	0	1.62	Open	–	Di Giacomo (2005)
Formosa	Thamnophilidae	*Taraba major*	25	0	5.96	Open	0.240	Di Giacomo (2005)
Formosa	Thamnophilidae	*Thamnophilus caerulescens*	8	0	2.85	Open	0.249	Di Giacomo (2005)
Formosa	Thraupidae	*Thraupis sayaca*	70	0	3.08	Open	0.108	Di Giacomo (2005)
Formosa	Troglodytidae	*Troglodytes aedon*	10	0	1.56	Closed (c)	0.177	Di Giacomo (2005)
Formosa	Turdidae	*Turdus amaurochalinus*	16	0	5.58	Open	0.171	Di Giacomo (2005)
Formosa	Tyrannidae	*Tyrannus melancholichus*	50	0	3.77	Open	0.234	Di Giacomo (2005)
Formosa	Vireonidae	*Vireo olivaceus*	5	0	1.78	Open	–	Di Giacomo (2005)
Formosa	Tyrannidae	*Xolmis cinerea*	30	0	5.58	Open	–	Di Giacomo (2005)
Formosa	Tyrannidae	*Xolmis irupero*	50	0	3.59	Closed (c)	–	Di Giacomo (2005)

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