

BROOD PARASITISM IN A HOST GENERALIST, THE SHINY COWBIRD: II. HOST SELECTION

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ABSTRACT.—Host selection by brood parasitic Shiny Cowbirds (*Molothrus bonariensis*) was studied at two sites in Buenos Aires Province, Argentina. The eggs of the parasite are either spotted or immaculate, so host selection was studied with respect to egg type as well as to site. Immaculate eggs were rare at both sites. Cowbirds in this region prefer to parasitize nests of birds larger than themselves. This preference contrasts with that of almost all other brood parasites, and even that of Shiny Cowbirds in other parts of the species' range. One large species, the Chalk-browed Mockingbird (*Mimus saturninus*) was used frequently and consistently at both sites. At least two other large species (thrushes) were used at Site I, but neither was present at Site II. Cowbirds were more specialized on large hosts at Site I: only 9% of the spotted eggs were laid in nests of small birds at Site I, whereas 35% were laid in such nests at Site II. Small species, such as the Rufous-collared Sparrow (*Zonotrichia capensis*), were used to a greater extent at Site II than Site I (where some of the same species were not used at all). The shift to smaller hosts is probably a response to a change in the structure of the community; large host species are relatively less abundant at Site II.

Rejecter species are large, and all were parasitized while many smaller acceptor species were unmolested. Surprisingly, more immaculate eggs were laid in nests where they had little chance of successful incubation, rather than in nests of acceptors. No evidence suggests that host races ("gentes") are formed. To the contrary, female cowbirds laying different egg types apparently select hosts in the same manner. Received 8 August 1984, accepted 25 July 1985.

SPECIES that use a wide variety of resources are known as generalists. The brood parasitic Shiny Cowbird (*Molothrus bonariensis*) is an extreme generalist with respect to the "host niche": its eggs have been found in nests of 201 species (Friedmann and Kiff 1985).

Our knowledge of how female cowbirds select hosts is incomplete and biased. First, data on parasitism are often gathered indirectly by studying a particular host species. Information about the composition of the host community and the rates of parasitism of other species is frequently unavailable. A second source of bias concerns the breeding seasons of host and parasite. In Tucumán Province, Argentina, only early nests of the Rufous-collared Sparrow (*Zonotrichia capensis*) escaped parasitism: all late nests were parasitized (King 1973). Third, several Shiny Cowbirds often parasitize a single nest (Friedmann 1929, 1963; Friedmann et al. 1977). The proportion of nests parasitized, the most frequently reported statistic, is an incom-

plete descriptor of parasitism in this case. A fourth bias concerns parasitism of species that reject cowbird eggs. Because rejecter species generally remove cowbird eggs in a very short time, parasitism of rejecters is unlikely to be observed (Rothstein 1971, 1975, 1977). Experiments simulating parasitism must have been performed previously to identify rejecters.

This study describes and interprets the contrasting patterns of host selection by Shiny Cowbird females at two sites in Buenos Aires Province, Argentina. Geographic variation in host selection remains unexplained. For example, parasitism of the Rufous-collared Sparrow (by the nominate subspecies of the cowbird) varies from 15 to 77% according to site (Sick 1958; King 1973; Fraga 1978, 1983; Gochfeld 1979; Salvador 1983).

I also present data on host selection with regard to egg color. Almost all eggs can be described as spotted or immaculate in eastern Argentina, Uruguay, and portions of Brazil. Intermediate eggs with a few fine spots are rare (Friedmann 1929; Fraga 1978, 1983, 1985; Gochfeld 1979; Salvador 1983). Some host species, dual acceptors, incubate both morphs. Other hosts, dual rejecters, remove all cowbird eggs

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from the nest. One major host (Chalk-browed Mockingbird, *Mimus saturninus*) is a differential accepter that ejects immaculate eggs but accepts spotted ones (Fraga 1980, 1985; Mason 1986). Several other important host species probably are differential accepters of cowbird eggs (Friedmann et al. 1977, Fraga 1985). These species are particularly important because they represent strong sources of natural selection on egg morphology and host selection. The ecological situation could potentially result in the evolution of host races or "gentes" (Payne 1977).

METHODS

One season was spent at each of two sites located 17.6 km apart near Magdalena, Buenos Aires Province, Argentina: Site I was Estancia San Isidro and Site II was Estancia El Talar. Further details, including the relative abundance of passerine species, are presented elsewhere (Mason 1985). The first season lasted from 20 October 1977 to 24 February 1978, and the second from 21 September 1978 to 10 February 1979. Very little laying by any passerine species occurs outside this interval (see below and Mason 1985). Nests were observed repeatedly until young fledged or activity at the nest ceased. Observations were carried out daily, although most nests were not observed with such frequency. Shiny Cowbird eggs were scored for color (spotted, immaculate, or intermediate), date, and host. A cohort of nests of the same species at each site was then characterized by a distribution describing the frequency of nests with a certain number of cowbird eggs of a specific type. Distributions obtained in this manner were compared using the heterogeneity G-test (Sokal and Rohlf 1981). Other statistical tests vary according to the particular comparison (see below). The diversity of host use at each site was described by calculating the Shannon-Weaver index (Peet 1974, Whittaker 1975).

Scientific names of species are given in the Appendix.

RESULTS

The data base consists of 360 nests (7 nest boxes) of 28 passerine species. I found 233 Shiny Cowbird eggs in nests of 13 species. The distribution of 212 spotted Shiny Cowbird eggs in 333 nests discovered in the egg phase is given in the Appendix. Species are listed by decreasing winglength of adult females (Mason 1980) because more accurate data for body size (i.e. weight) are lacking. Both intensity (mean number of cowbird eggs per parasitized nest) and frequency of parasitism (percentage of nests

parasitized) are reported because many nests were multiply parasitized. Eggs laid in peculiar circumstances (such that they could not be scored for acceptance or rejection), and eggs found in nests but later rejected are included.

Only 15 immaculate and 6 intermediate eggs with a few fine spots were seen. Intermediate eggs appear immaculate from a distance of about 1 m or more. The Chalk-browed Mockingbird, the only species known to respond differentially to different egg morphs (Fraga 1985, Mason 1986), apparently perceives intermediate eggs as immaculate (see below).

Comparisons between sites.—Immaculate and intermediate eggs were rare at both sites. At Site I, I found 4 immaculate eggs, 0 intermediate eggs, and 8 spotted eggs in nests of dual accepters. At Site II, I found 0 immaculate eggs, 1 intermediate egg, and 53 spotted eggs in such nests.

At both sites, species larger than the cowbird were preferred as hosts (Site I: $G = 57.6$, 7 df, $P < 0.001$; Site II: $G = 34.0$, 7 df, $P < 0.001$). The mockingbird was the only large species present at both sites and represented by samples sufficient for statistical comparison; it was parasitized equally at each site ($G = 13.3$, 9 df, $P > 0.1$). All thrush nests were parasitized. In addition to the 5 nests found in the egg stage (see Appendix), an additional nest of each species each contained 2 cowbird young.

At Site I, large, abundant passerines (excluding the mockingbird) were: Rufous Hornero (a dual rejecter), Great Kiskadee (response to spotted cowbird eggs uncertain; Mason 1986), Rufous-bellied Thrush, White-rumped Swallow (body size considerably smaller than that of the cowbird, but included because of its winglength), and the Brown-and-yellow Marshbird [*Pseudoleistes virescens*; no nests found, but a frequent host choice in Buenos Aires (Gibson 1918; Hudson 1920; Friedmann 1929, 1963; Friedmann et al. 1977)]. At Site II, the thrush was absent and the Brown-and-yellow Marshbird rare (Mason 1985). Excluding the small-bodied swallow, only 1 large accepter of spotted eggs (the mockingbird) was abundant at Site II, as opposed to at least 2 (mockingbird, thrush) but probably 3 (including the marshbird) such species at Site I.

The sites differed markedly in that species smaller than the cowbird were used to a much greater extent at Site II. The Rufous-collared Sparrow was used significantly more at Site II

than at Site I ($G = 9.7$, 3 df, $P < 0.01$). Two other species (Yellow-browed Tyrant, House Wren) were ignored by cowbirds at Site I, but both were parasitized at Site II, although sample sizes are small. The tyrant, wren (natural nest sites), and sparrow were used equally at Site II ($G = 4.4$, 6 df, $P > 0.50$). In addition, the Bay-winged Cowbird was used more at Site II than at Site I, and a single spotted cowbird egg was laid in a nest of the Freckle-breasted Thornbird at Site II the day following loss of that nest. Only 1 small species (Saffron Finch) was parasitized at Site I but not Site II. When frequencies for all small species with data from both sites were pooled, smaller species were parasitized significantly more often ($G = 16.9$, 5 df, $P < 0.005$).

House Wrens at Site II nesting in boxes were more heavily parasitized than those nesting in natural sites ($G = 17.30$, 5 df, $P < 0.05$). A pair of wrens used a nest box at Site I, but this nest was not parasitized. The only other use of a nest box was by a pair of Saffron Finches (Site II).

Cowbirds selected a more diverse array of hosts at Site II than at Site I (measured by the Shannon-Weaver index; Peet 1974, Whittaker 1975), regardless of whether hosts were characterized by species or by size (Table 1). The latter analysis was done because a cowbird's decision to parasitize a nest may be based on some general aspect, such as size, rather than on species identity (Rothstein 1976).

Parasitism of rejecters.—Although I could not estimate the true frequency of parasitism of rejecters, I observed some cowbird eggs in nests of the Rufous Hornero and the Fork-tailed Flycatcher (both dual rejecters; Fraga 1980, Mason 1986). Responses could not be scored in 3 cases of parasitism of the hornero because I accidentally destroyed one nest, or the cowbird egg was laid extremely late in the incubation or nestling period. Two spotted eggs were rejected and later found, one in the entrance of a nest and the other directly below a nest. A broken eggshell was found below another nest, probably from an egg laid and rejected between observations. Four nests of the Fork-tailed Flycatcher contained cowbird eggs. Two nests had 3 cowbird eggs each (1 of which was intermediate), and all eggs were ejected. Neither nest was ever known to contain host eggs. Two other nests each received 1 spotted egg, which was ejected in both cases.

The Chalk-browed Mockingbird, unlike the

TABLE 1. Diversity in host selection by site.^a

	p_i	$-p_i \log p_i$
Host diversity measured by species		
Site I		
Rufous Hornero	0.013	0.024
Cattle Tyrant	0.013	0.024
Chalk-browed Mockingbird	0.759	0.091
Rufous-bellied Thrush	0.127	0.114
Creamy-bellied Thrush	0.013	0.024
Bay-winged Cowbird	0.025	0.040
Saffron Finch	0.013	0.024
Rufous-collared Sparrow	0.038	0.054
	$H' = 0.395^b$	
Site II		
Rufous Hornero	0.022	0.037
Freckle-breasted Thornbird	0.007	0.016
Yellow-browed Tyrant	0.030	0.045
Cattle Tyrant	0.007	0.016
Fork-tailed Flycatcher	0.052	0.067
White-rumped Swallow	0.037	0.053
House Wren	0.059	0.073
House Wren (nest boxes)	0.141	0.120
Chalk-browed Mockingbird	0.533	0.146
Bay-winged Cowbird	0.015	0.027
Rufous-collared Sparrow	0.096	0.098
	$H' = 0.698$	
Host diversity measured by size^c		
Site I		
Large	0.911	0.037
Small	0.089	0.093
	$H' = 0.130$	
Site II		
Large	0.644	0.123
Small	0.356	0.160
	$H' = 0.283$	

^a p 's represent the proportion of spotted eggs found in nests of different species.

^b Host diversity measured using the Shannon-Weaver index (Whittaker 1975): $H' = -\sum p_i \log p_i$.

^c Large and small reckoned using winglength relative to the Shiny Cowbird.

hornero and the flycatcher, generally rejects immaculate eggs. Thirteen immaculate and intermediate eggs were observed in 10 mockingbird nests. Three were accepted, 7 ejected, and the remainder could not be scored (predation or collection). At one nest where acceptance was observed, an immaculate egg was rejected the previous day.

Rejecter species of South America resemble North American rejecters in being large. Rejecters (of at least one morph) are, on average, larger than accepter species (Table 2; $P < 0.05$, Mann-Whitney $U = 5$; Siegel 1956). This test,

TABLE 2. Passerine size (estimated by winglength) and response to cowbird eggs.

Wing-length ^a	Species	Response to eggs ^b	
		Spotted	Immaculate
138	Brown-chested Martin	Acc	Acc
129	Great Kiskadee ^c	?	Acc
126	Chalk-browed Mockingbird	Acc	Rej
125	Rufous-bellied Thrush ^c	Acc?	Rej?
123	Creamy-bellied Thrush	Acc	Acc
119	White-rumped Swallow	Acc	Acc
112	Fork-tailed Flycatcher	Rej	Rej
107	Rufous Hornero	Rej	Rej
104	Shiny Cowbird		
99	Cattle Tyrant	Acc	Acc
98	Blue-and-yellow Tanager	Acc	Acc
93	Bay-winged Cowbird	Acc	Acc
90	Yellow-browed Tyrant	Acc	Acc
85	Firewood-gatherer	Acc	Acc
81	Vermillion Flycatcher	Acc	Acc
73	House Sparrow	Acc	Acc
71	Grassland Yellow-Finch	Acc	Acc
70	Freckle-breasted Thornbird	Acc	Acc
67	Rufous-collared Sparrow	Acc	Acc
66	Saffron Finch	Acc	Acc
64	Tufted Tit-Spintail	Acc	Acc
63	Wren-like Rushbird	Acc	Acc
63	Little Thornbird	Acc	Acc
57	Grassland Sparrow	Acc	Acc
51	House Wren	Acc	Acc
51	Masked Gnatcatcher	Acc	Acc
48	White-crested Tyrannulet	Acc	Acc

^a Rejecters are significantly larger than accepters (Mann-Whitney *U*-test, $P < 0.05$, $U = 5$). Large and small reckoned relative to the Shiny Cowbird.

^b Acc = accepts, Rej = rejects (Mason 1986).

^c Not included in the analysis because response to cowbird eggs not verified experimentally.

based on winglength, is conservative because it includes as large birds two Hirundinidae (White-rumped Swallow, Brown-chested Martin), birds with extremely long wings relative to body size.

Seasonality.—The first cowbird egg was laid on 7 October and the last on 19 January (Fig. 1). Three species, all furnariids (Rufous Hornero, Firewood-gatherer, Freckle-breasted Thornbird), completed a portion of their breeding before the cowbird (Mason 1985). The last two species accept all cowbird eggs (Mason 1986), but only a single nest of the thornbird was parasitized (see Appendix). Nests of the Rufous Hornero were ranked by date: parasitized nests occurred later in the season (Mann-Whitney $U = 8$, $P < 0.025$; Siegel 1956).

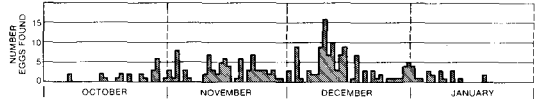


Fig. 1. Dates that cowbird eggs were laid or found.

The breeding seasons of the Chalk-browed Mockingbird and the Rufous-collared Sparrow were completely within the breeding season of the cowbird. I divided the breeding seasons of these two hosts into quarters and tested for heterogeneity among the subsamples. For the mockingbird, I pooled both sites because the distributions were equivalent. For the sparrow, parasitism only from Site II was analyzed. The subsamples provided no evidence of heterogeneity in either species (mockingbird: $G = 27.4$ for 27 df, NS, $0.25 < P < 0.5$; sparrow: $G = 9.2$ for 9 df, NS, $0.25 < P < 0.5$).

DISCUSSION

The extent of generalization by Shiny Cowbirds varied between two sites. Most large species apparently were used consistently, regardless of response to cowbird eggs. Use of smaller species was variable, but more prevalent at Site II. The Chalk-browed Mockingbird was parasitized consistently and heavily at both sites. Other large hosts (thrushes) were parasitized at Site I, but were absent from Site II. The Brown-and-yellow Marshbird, probably a common host in Buenos Aires Province (Hudson 1874, 1920; Sclater and Hudson 1888; Gibson 1918; see reviews by Friedmann 1929, 1963, and Friedmann et al. 1977), was abundant at Site I but rare at Site II.

The Shannon-Weaver indices (Table 1) describe the width of the "host niche" and illustrate differences in site-specific host selection. Although the measurements were determined in part by my ability to find and examine nests, the occasional or rare parasitism of a few species not censused would result in only slight changes. If I missed common, heavily parasitized species, the indices would be substantially altered. The only species likely in this category is the Brown-and-yellow Marshbird at Site I. If this species was heavily parasitized, the index (reckoned by species) would increase at Site I, decreasing the difference between sites. If reckoned by size, however, the index would increase the contrast because the marshbird is a large species (Mason 1980).

Conspicuousness might predispose a nest to parasitism (Brown-headed Cowbird, *Molothrus ater*: Nice 1937, Rothstein 1975; Shiny Cowbird: Friedmann 1929, 1963; Gochfeld 1979), but the contrast between sites in parasitism of the Rufous-collared Sparrow and other small species argues against the importance of conspicuousness. The elaborate nests of furnariids (e.g. the hornero, Firewood-gatherer, and thornbirds) are conspicuous to the human observer, but these are not equally likely to be parasitized. Birds that nest in old hornero nests (Tufted Tit-Spinetail, White-rumped Swallow, Saffron Finch, House Sparrow) were likewise not equally parasitized despite the control for nest site (Appendix; Mason 1985). The strongest support for the conspicuousness argument is the significant difference (at Site II) in parasitism of wrens nesting in boxes as opposed to natural nesting sites.

A more satisfying explanation attributes the local differences to the operation of the same host-selection mechanism in environments offering differing arrays of resources (hosts). Preference measures have different formal descriptions (Ivlev 1961, Murdoch 1969, Rapport and Turner 1970, Chesson 1978, Jaenike 1980), but none can be calculated here because precise numerical densities of host and parasite populations are unavailable. Nonetheless, three distinct lines of evidence provide qualitative support that large hosts are preferred: (1) among accepters, larger hosts were parasitized more frequently and to a greater extent than were smaller hosts; (2) all known rejecter species (which are large) were parasitized while many accepters were left unmolested; and (3) when larger hosts were less abundant or absent, cowbirds used smaller hosts.

Niche expansion and inclusion of species like the sparrow is probably adaptive. Pecking of host eggs by cowbirds is a density-dependent form of mortality that sometimes terminates nesting attempts. Pecking depresses the survivorship of mockingbird nests to a level indistinguishable from that of the Rufous-collared Sparrow (Mason 1986). Presumably, if niche width remained constant in the two environments, nest losses to pecking would further increase at Site II, and cowbirds would experience still lower success.

Other studies share a common feature that supports the claim of a preference for larger hosts: at least one large host is heavily used,

while the small Rufous-collared Sparrow is parasitized less. During the last half of a 10-yr study of the sparrow at Lobos, Buenos Aires (Fraga 1978, 1983), parasitism dropped significantly from 72.5 to 43.5%. This coincided with changes in local agriculture that attracted the White-browed Blackbird (*Sturnella supercilialis*), a bird much larger than the sparrow. Two of 6 nests contained cowbird eggs, but the species was seen tending cowbird fledglings (Fraga 1985). Parasitism of the mockingbird remained high (above that of the sparrow; Fraga 1985) and unchanged. In Villa María, Córdoba Province, the mockingbird was used more than any other local host (86.9% of nests parasitized; Salvador 1983). Other large hosts also were used, but only 8 of 22 Rufous-collared Sparrow nests held cowbird eggs. With regard to the parasitism of this host, Salvador wrote: "at this site, it [the sparrow] was not a host of great importance, if we compare it with *Mimus saturninus*" [Salvador 1983: 155 (trans. by PM)].

Gochfeld (1979) found heavy use (23/24 nests) of the Long-tailed Meadowlark (*Sturnella loyca*) but no use (0/11) of the highly similar Lesser Red-breasted Meadowlark (*Sturnella defilippi*) in Bahía Blanca, southern Buenos Aires Province. The low frequency of parasitism of the Rufous-collared Sparrow (2/13 nests) resembles my results at Site I, but 0 of 4 nests of mockingbirds contained cowbird eggs (Gochfeld pers. comm.). Both types of eggs occurred at the site. The absence of parasitic eggs in mockingbird and Lesser Red-breasted Meadowlark nests may possibly reflect rejection behavior of the hosts rather than avoidance by cowbirds.

The preference for large hosts, a trait unusual in any parasitic bird (Payne 1977), may be a phenomenon restricted to the Río de La Plata basin and surrounding area. In the West Indies, there is no clear relationship between host size and preference ranking by Shiny Cowbirds. In Trinidad the diminutive House Wren may be the most highly preferred host (Manolis 1982), while in Puerto Rico both large and small hosts may be heavily used (Pérez Rivera 1983, Wiley 1985).

Host selection by females laying contrasting egg types.—Only 5 immaculate and intermediate eggs were laid in nests of accepters, whereas 16 were laid in nests of species that normally reject these morphs. Females that lay these eggs clearly do not place them preferentially in nests

where the eggs will be accepted. No evidence suggests that host selection varies between females.

Fraga (1985) also described immaculate eggs laid in and rejected from mockingbird nests. He estimated that at least one-third of the nests were parasitized with white eggs. Descriptions of immaculate eggs below, but spotted eggs inside, nests of the Brown-and-yellow Marshbird (Hudson 1874, 1920; Sclater and Hudson 1888) suggest that this host is a differential acceptor like the mockingbird and that cowbirds behave the same toward the marshbird and the mockingbird. This pattern of host selection is apparently stable because Hudson's observations were conducted more than a century ago.

Parasitism of rejecters.—Parasitism of rejecter species poses a significant and interesting evolutionary problem. Selection penalizes females that lay either egg morph when they lay in nests of dual rejecters. However, oviposition in nests of differential acceptors penalizes only certain females. The situation is complex because selection occurs on a phenotype (the morphology of the egg) that is a product of the maternal genotype.

The frequency of oviposition in nests of rejecters suggests that host race formation does not occur in Shiny Cowbirds. Females that lay in nests of rejecters almost certainly did not fledge from nests of those species. Similarly, it seems unlikely that all females laying immaculate eggs in mockingbird nests hatched from spotted eggs laid in mockingbird nests, although this possibility cannot be ruled out. In addition, production of cowbird offspring may be highest for hosts of low-preference ranking. Fraga (1985) presented data that more cowbirds fledged from nests of Rufous-collared Sparrows than of Chalk-browed Mockingbirds, and he argued that most females laying in mockingbird nests probably fledged from nests of other species.

The host selection mechanism is clearly under natural selection, but response to selection requires (among other things) that there exist proximate cues for ultimate success. Apparently, these cues are often lacking, at least in this environment. Some features of Shiny Cowbird parasitism, such as inclusion of the sparrow in the array of host choices, appear to be subtle adaptations (Mason 1986). Other features, such as the parasitism of rejecters, remain perplexing.

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APPENDIX. Parasitized and unparasitized nests.

Wing-length ^a	Species	No. of cowbird eggs per nest ^b										Freq. ^c	Int. ^d	
		0	1	2	3	4	5	6	7	8	9			10
A. Distribution, frequency, and intensity of parasitism														
126	Chalk-browed Mockingbird (<i>Mimus saturninus</i>)													
	Site I (n = 30)	8	8	6	5	0	0	0	1	1	0	1	0.73	2.73
	Site II (n = 38)	10	9	6	6	3	3	1					0.74	2.57
125	Rufous-bellied Thrush (<i>Turdus rufiventris</i>)													
	Site I (n = 4)	0	2	1	0	0	1						1.00	2.25
	Site II	Species absent												
123	Creamy-bellied Thrush (<i>T. amaurochalinus</i>)													
	Site I (n = 1)	0	1										1.00	1.00
	Site II	Species absent												
119	White-rumped Swallow (<i>Tachycineta leucorrhoa</i>)													
	Site I (n = 1)	1											0.00	—
	Site II (n = 9)	5	3	1									0.44	1.25
112	Fork-tailed Flycatcher (<i>Tyrannus savana</i>) ^e													
	Site I	No nests examined												
	Site II (n = 7)	3	2	1	1								0.57	1.75
107	Rufous Hornero (<i>Furnarius rufus</i>) ^e													
	Site I (n = 1)	0	1										1.00	1.00
	Site II (n = 16)	13	3										0.19	1.00
104	Shiny Cowbird (<i>Molothrus bonariensis</i>)													
99	Cattle Tyrant (<i>Machetornis rixosus</i>)													
	Site I (n = 1)	0	1										1.00	1.00
	Site II (n = 2)	1	1										0.50	1.00
93	Bay-winged Cowbird (<i>Molothrus badius</i>)													
	Site I (n = 10)	8	2										0.20	1.00
	Site II (n = 5)	3	2										0.40	1.00
90	Yellow-browed Tyrant (<i>Satrapa icterophrys</i>)													
	Site I (n = 2)	2											0.00	—
	Site II (n = 8)	4	4										0.50	1.00
70	Freckle-breasted Thornbird (<i>Phacelodorus striaticollis</i>)													
	Site I (n = 3)	3											0.00	—
	Site II (n = 4)	3	1										0.25	1.00
67	Rufous-collared Sparrow (<i>Zonotrichia capensis</i>)													
	Site I (n = 32)	29	3										0.09	1.00
	Site II (n = 19)	11	5	1	2								0.42	1.63
66	Saffron Finch (<i>Sicalis flaveola</i>)													
	Site I (n = 13)	12	1										0.08	1.00
	Site II (n = 22)	22											0.00	—

APPENDIX. Continued.

Wing-length ^a	Species	No. of cowbird eggs per nest ^b										Freq. ^c	Int. ^d	
		0	1	2	3	4	5	6	7	8	9			10
51	House Wren (<i>Troglodytes aedon</i>)													
	Natural nest sites													
	Site I (n = 3)	3											0.00	—
	Site II (n = 8)	3	3	1	1								0.63	1.60
	Nest boxes													
	Site I (n = 1)	1											0.00	—
	Site II (n = 5)	0	0	2	0	2	0	0	1				1.00	3.80
B. Species not observed to be parasitized^f														
138	Brown-chested Martin (<i>Phaeoprogne tapera</i>) (0, 1)													
129	Great Kiskadee (<i>Pitangus sulphuratus</i>) ^e (0, 7)													
85	Firewood-gatherer (<i>Anumbius annumbi</i>) (0, 11)													
81	Vermillion Flycatcher (<i>Pyrocephalus rubinus</i>) (0, 22)													
73	House Sparrow (<i>Passer domesticus</i>) (0, 3)													
71	Grassland Yellow-Finch (<i>Sicalis luteola</i>) (0, 3)													
69	Hooded Siskin (<i>Carduelis magellanica</i>) (0, 7)													
64	Tufted Tit-Spinetail (<i>Leptasthenura platensis</i>) (1, 3)													
63	Wren-like Rushbird (<i>Phleocryptes melanops</i>) (0, 22)													
63	Little Thornbird (<i>Phacellodomus sibilatrix</i>) (1, 0)													
57	Grassland Sparrow (<i>Ammodramus humeralis</i>) (0, 1)													
51	Masked Gnatcatcher (<i>Poliophtila dumicola</i>) (0, 1)													
48	White-crested Tyrannulet (<i>Serpophaga subcristata</i>) (1, 3)													
?	Tropical Kingbird (<i>Tyrannus melancholicus</i>) (1, 0)													
?	Pipit (<i>Anthus</i> sp.) (0, 1)													

^a Species listed by decreasing winglength (measured from skins of adult females collected in Buenos Aires Province; Mason 1980).

^b Spotted eggs only.

^c Freq. = frequency (proportion of nests parasitized).

^d Int. = intensity (mean number of eggs per parasitized nest).

^e *Tyrannus savana* and *Furnarius rufus* rejected cowbird eggs. *Pitangus sulphuratus* may show intermediate levels of rejection. Some birds were not tested for response to cowbird eggs (Mason 1986).

^f Sample sizes for sites I and II in parentheses.