BROOD PARASITISM IN A HOST GENERALIST, THE SHINY COWBIRD: I. THE QUALITY OF DIFFERENT SPECIES AS HOSTS

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ABSTRACT.—The Shiny Cowbird (*Molothrus bonariensis*) of South America, Panama, and the West Indies is an obligate brood parasite known to have used 176 species of birds as hosts. This study documents wide variability in the quality of real and potential hosts in terms of response to eggs, nestling diet, and nest survivorship. The eggs of the parasite are either spotted or immaculate in eastern Argentina and neighboring parts of Uruguay and Brazil. Most species accept both morphs of cowbird eggs, two reject both morphs, and one (Chalk-browed Mockingbird, *Mimus saturninus*) rejects immaculate eggs but accepts spotted ones. No species, via its rejection behavior, protects the Shiny Cowbird from competition with a potential competitor, the sympatric Screaming Cowbird (*M. rufoaxillaris*). Cross-fostering experiments and natural-history observations indicate that nestling cowbirds require a diet composed of animal protein. Because most passerines provide their nestlings with such food, host selection is little restricted by diet. Species-specific nest survivorship, adjusted to appropriate values of Shiny Cowbird life-history variables, varied by over an order of magnitude. Shiny Cowbirds peck host eggs. This density-dependent source of mortality lowers the survivorship of nests of preferred hosts and creates natural selection for greater generalization. Host quality is sensitive to the natural-history attributes of each host species and to the behavior of cowbirds at nests. *Received 4 June 1984, accepted 26 June 1985.*

VARIATION in resource quality can have great ecological and evolutionary consequences. Obligate brood parasites never build nests but leave the care of their eggs and young to other species, their hosts. The parental behavior of hosts is a critical and quantifiable resource to brood parasites. The first task in understanding the use of resources is to ascertain the quality of each alternative. I surveyed the quality of various passerine species as hosts of the Shiny Cowbird (*Molothrus bonariensis*) in Buenos Aires Province, Argentina. Host quality is tractable to analysis because selection is spatially and temporally focused at nests. Dimensions of host quality examined include response to parasitic eggs, nestling diet, and characteristic survivorship of each species' nests. This is the only systematic attempt to characterize the quality of an array of species for any brood parasite.

The Shiny Cowbird is widely distributed throughout South America (Friedmann 1929). It is an extreme host generalist, known to have parasitized 176 species (Friedmann et al. 1977). The Shiny Cowbird is sympatric with a potential competitor, the Screaming Cowbird (*M. rufoaxillaris*), in Argentina, Uruguay, and neighboring parts of South America. This latter species is extremely specialized on the cooperatively nesting Bay-winged Cowbird (*M. badius*), although anecdotal reports of its use of other hosts exist (Hudson 1874, 1920; Grant 1911, 1912; Pereyra 1938; Hoy and Ottow 1964).

Experiments that simulate natural parasitism provide two kinds of important information. First, the technique identifies individuals that reject parasitic eggs. This response is apparently species typical for North American birds (Rothstein 1975a, b). Rejecter species can easily be regarded as unsuitable to cowbirds on the basis of this single criterion (Rothstein 1982). Second, if a species is an accepter, then observed parasitism accurately reflects use of that species. If both Shiny Cowbird and Screaming Cowbird eggs appear in nests, the two parasitic species are potentially in competition. Experiments in artificial parasitism can reveal if certain species reject eggs of one species but accept those of the other.

Categorization of species as accepters or re-

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jecters is complicated by extreme variation in Shiny Cowbird eggs. Some species may reject one egg type but accept many others. Despite the unusual level of variation, two broad classes of eggs are recognized: spotted and immaculate (Friedmann 1929, Fraga 1978, Gochfeld 1979). More importantly, I found no evidence that birds discriminated against eggs within each category, and this is the primary justification for the dichotomous categorization (see Results). Screaming Cowbird eggs (described in detail by Fraga 1983a) are spotted, but the maculations are less distinct. Most also possess miniscule scrawls.

Nestling diet is another critical aspect of host quality. Cross-fostering, the introduction of parasitic young into nests, is a difficult but informative technique capable of assessing host dietary quality. Failing this, descriptions of food items brought to nests may be adequate.

Nests are subject to total failure for reasons such as predation and severe weather. Survivorship estimates are appropriate measures of this aspect of host quality.

Methods

Observations were carried out almost daily for two seasons (1977–1978 and 1978–1979) at two sites 17.6 km apart near Magdalena, Buenos Aires Province, Argentina. Descriptions of the study sites, the avifauna, and my general field techniques appear elsewhere (Mason 1985). The habitat consisted of pasture, with clumps of trees and marsh. I searched continually for nests to carry out manipulations and make observations. Of course, nests that were difficult to find or examine are underrepresented in the sample.

The technique of artificial parasitism followed Rothstein (1971), except that I occasionally placed 2 eggs in a single nest. The experiments used real and artificial eggs of 3 experimental morphs: spotted *M. bonariensis*, white *M. bonariensis*, and *M. rufoaxillaris*. Dimensions and weights of real and artificial eggs can be found in Mason (1980). Experimental parasitism was performed as early as possible, and always before 1200. This corresponds to the natural laying behavior of Shiny Cowbird females (Hoy and Ottow 1964).

There are two mutually exclusive responses to parasitic eggs: acceptance for incubation, or rejection. Rejection includes any behavior of the host species that does not result in successful incubation: ejection of the parasitic egg, nest desertion, or burial of the parasitic egg. I scored an experimentally placed egg as accepted if it remained in the nest 5 days or more (see Rothstein 1975a). Large series of experiments with North American bird species indicate that almost all rejections occur within this period (Rothstein 1975a, Mason unpubl. data).

Species were categorized as accepters or rejecters for specific egg types if two-thirds or more of the responses were consistent. Usually, responses are more consistent, but Rothstein (1975b) used this truncation criterion to show that species' responses were distributed bimodally. Species were not categorized if the frequency of rejection fell between one-third and two-thirds. Species were tentatively regarded as accepters of any egg morph with which they were not tested if (1) the species clearly accepted cowbird eggs widely divergent from its own eggs; or (2) the untested morph closely resembled its own. For example, a species laying an immaculate white egg and shown experimentally to accept spotted eggs would be tentatively categorized as an accepter of immaculate cowbird eggs.

To assess dietary quality and response to nestlings, I augmented observations of nestling development with cross-fostering experiments. If a nestling cowbird remained healthy on subsequent visual inspections, dietary quality was scored as acceptable. Unhealthy birds were recognized by any of the following symptoms: pallor, emaciation, loss of thermoregulatory ability, or moribund passivity. Ideally, cross-fostered cowbirds should be larger than host young to eliminate the possibility that subsequent starvation of the cowbird is the result of a competitive disadvantage and not of dietary quality.

Host species were scored as acceptable with respect to diet if cross-fostered nestlings fledged. If nestlings appeared healthy before nest failure (occurring for reasons unrelated to parasitism), the host was scored as tentatively acceptable.

Nest survivorship can estimate the parasite's expectation of success, provided the host fulfills the other requirements for acceptability. I measured the probability of survival for the egg and nestling phases, considering only those sources of mortality that affected all nest occupants similarly and simultaneously. Survivorship of each interval was calculated by raising daily survivorship to a power equal to the length of that interval in days (Mayfield 1975, Hensler and Nichols 1981). Because cowbirds differ from most of their hosts in length of the incubation and nestling periods, I used the appropriate values of these Shiny Cowbird life-history variables (11.9 days and 13.9 days, respectively; Mason unpubl. data) to find the specific value of the host to cowbirds. The length of the egg phase includes the laying period of the host as well as the incubation period of the cowbird egg. Survivorship to fledging is the product of survivorship during the egg and the nestling phases. The survivorship estimates reflect freedom of the nest

TABLE 1. Passerine response to cowbird eggs. Experimental eggs were of 3 morphs: immaculate Shiny Cowbird (Shiny, I), spotted Shiny Cowbird (Shiny, S), and Screaming Cowbird (Screaming).

Host species[b]	Response to experimental egg morphs[a]		
	Shiny, I	Shiny, S	Screaming
	R/T (Status)	R/T (Status)	R/T (Status)
Rufous Hornero, *Furnarius rufus* (I)	4/5 (Rej)	5/6 (Rej)	4/4 (Rej)
Wren-like Rushbird, *Phleocryptes melanops* (I)	0/5 (Acc)	0/7 (Acc)	0/4 (Acc)
Tufted Tit-Spinetail, *Leptasthenura platensis* (I)	0/1 (Acc)	0/4 (Acc)	0/2 (Acc)
Little Thornbird, *Phacellodomus sibilatrix* (I)	— (Acc?)[c]	0/1 (Acc)	— (Acc?)
Freckle-breasted Thornbird, *Phacellodomus striaticollis* (I)	— (Acc?)	0/1 (Acc)	0/2 (Acc)
Firewood-gatherer, *Anumbius annumbi* (I)	— (Acc?)	0/6 (Acc)	0/4 (Acc)
Vermillion Flycatcher, *Pryocephalus rubinus* (S)	0/6 (Acc)	0/6 (Acc)	0/3 (Acc)
Yellow-browed Tyrant, *Satrapa icterophrys* (S)	1*/3[d] (Acc)	0/2 (Acc)	0/1 (Acc)
Cattle Tyrant, *Machetornis rixosus* (S)	0/2 (Acc)	— (Acc?)	— (Acc?)
Fork-tailed Flycatcher, *Tyrannus savana* (S)	3/3 (Rej)	2/2 (Rej)	— (Rej?)
Great Kiskadee, *Pitangus sulphuratus* (S)	0/4 (Acc)	1/2 ?	1/2 ?
White-crested Tyrannulet, *Serpophaga subcristata* (I)	— (Acc?)	0/1 (Acc)	0/1 (Acc)
House Wren, *Troglodytes aedon* (S)	0/3 (Acc)	— (Acc?)	— (Acc?)
White-rumped Swallow, *Tachycineta leucorrhoa* (I)	— (Acc?)	0/3 (Acc)	0/1 (Acc)
Brown-chested Martin, *Phaeoprogne tapera* (I)	— (Acc?)	0/1 (Acc)	— (Acc?)
Chalk-browed Mockingbird, *Mimus saturninus* (S)	8*/11 (Rej)	2*/10 (Acc)	6/12 ?
Creamy-bellied Thrush, *Turdus amaurochalinus* (S)	0/1 (Acc)	— (Acc?)	— (Acc?)
Masked Gnatcatcher, *Polioptila dumicola* (S)	0/1 (Acc)	— (Acc?)	— (Acc?)
Bay-winged Cowbird, *Molothrus badius* (S)	0/6 (Acc)	— (Acc?)	0/1 (Acc)
Blue-and-yellow Tanager, *Thraupis bonariensis* (S)	0/1 (Acc)	— (Acc?)	0/1 (Acc)
Saffron Finch, *Sicalis flaveola* (S)	0/4 (Acc)	0/8 (Acc)	2**/8 (Acc)
Grassland Yellow-Finch, *Sicalis luteola* (S)	0/2 (Acc)	— (Acc?)	— (Acc?)
Grassland Sparrow, *Ammodramus humeralis* (S)	0/1 (Acc)	— (Acc?)	— (Acc?)
Rufous-collared Sparrow, *Zonotrichia capensis* (S)	2**/6 (Acc)	1*/5 (Acc)	0/7 (Acc)
Hooded Siskin, *Carduelis magellanica* (S or I)	— ?	0/1 (Acc)	0/1 (Acc)
House Sparrow, *Passer domesticus* (S)	0/1 (Acc)	0/1 (Acc)	— (Acc?)

[a] R/T represents the number of rejections out of the number of trials. Acc = accepts, Rej = rejects.

[b] Common names according to Meyer de Schauensee (1970). The letter in parentheses following each species name roughly categorizes the eggs of that species as spotted (S) or immaculate (I). More detailed descriptions of eggs are in Mason (1985).

[c] Species that accepted eggs widely divergent from their own, but untested for morphs more similar to their own, are tentatively scored as accepters, as indicated by a question mark.

[d] Each asterisk indicates a case of desertion.

from complete loss, but do not include events that cause differential mortality within the nest.

Scientific names of species are given in Table 1.

RESULTS

Responses to eggs.—I performed 187 experimental egg manipulations and scored 42 responses as rejections. Species could almost always be categorized as accepters or rejecters, although only for a specific egg morph in the case of the Chalk-browed Mockingbird (Table 1). Species classified as rejecters of all eggs (Rufous Hornero, Fork-tailed Flycatcher) may be referred to as dual rejecters, and those classified as accepters of all as dual accepters. The Chalk-browed Mockingbird is a differential accepter, favoring the spotted Shiny Cowbird egg morph. Two species, the Chalk-browed Mockingbird and the Great Kiskadee, showed intermediate levels of ejection for certain morphs. In the case of the kiskadee, the problem may be one of small sample sizes (4 experiments with spotted eggs), but this is not true for the mockingbird, which rejected Screaming Cowbird eggs from 6 of 12 nests. I have not assigned rejecter or accepter status to either species.

Eight rejections occurred by desertion and none by egg burial. Unlike ejection, desertion was never expressed consistently. No species could be classified as a rejecter on the basis of desertion.

No evidence suggests that response to artificial eggs differs from response to natural eggs. To use the Chalk-browed Mockingbird as an example, responses to real and artificial eggs

TABLE 2. Results of cross-fostering experiments. Number of experiments for each host species is indicated in parentheses. See text for discussion.

Host species	Results
Rufous Hornero (1)	4-day-old nestling lived 4 more days before starvation, losing in competition with much bigger host nestlings
Firewood-gatherer (1)	Lived 3–4 days before death of all nestlings due to botfly parasitism
Vermillion Flycatcher (1)	Lived 2–3 days until predation
Yellow-browed Tyrant (1)	Lived 5 days until predation
Great Kiskadee (1)	Nestling of several days fledged after 9 more days in nest
Chalk-browed Mockingbird (2)	Nestling at first nest lived 4–5 days until predation at nest; nestling at second nest lived 6–7 days until predation at nest
Creamy-bellied Thrush (1)	Fledged after 14–15 days in nest, but at very low weight, having hatched 4 days after host nestling
Saffron Finch (2)	Nestling Shiny Cowbird lived 2 days until death of all nestlings due to botfly parasitism; nestling Screaming Cowbird failed within 2 days
House Sparrow (1)	Failed within 2 days

were statistically indistinguishable ($P > 0.5$ for all comparisons among immaculate and spotted Shiny Cowbird eggs and Screaming Cowbird eggs; Fisher's exact test, Siegel 1956). Furthermore, the assignment of species as accepters or rejecters (Table 1) agrees with Fraga (1978, 1980, 1983b, 1985) for 11 common species, including all rejecters. Observations of natural parasitism agree (Mason 1986).

Lack of competition from the Screaming Cowbird.—In all but one case (Chalk-browed Mockingbird), birds responded to Screaming Cowbird eggs as they did to spotted Shiny Cowbird eggs. No host species totally protects the Shiny Cowbird from competition with the Screaming Cowbird via its rejection behavior. Since Screaming Cowbird eggs were found only in nests of the Bay-winged Cowbird (Mason 1980), host selection in the Shiny Cowbird is unaffected by nestling competition with the former species in all other nests.

Nestling diet.—I performed 11 cross-fostering experiments (Table 2). Only 2 species were scored as having unacceptable diets: the Saffron Finch and the House Sparrow. Observations of natural parasitism support the experiments in the case of the finch: 2 Shiny Cowbirds in separate nests both failed to survive 2 days. No fledging records exist for either species. The remaining species were judged as acceptable, and observations support this interpretation. Differential mortality of the cowbird nestling occurred at 1 nest of the Rufous Hornero, and 1 nest of the Creamy-bellied Thrush. Both deaths were attributed to intranest competition because host young had a substantial size advantage (Table 2). The hornero has been known to rear cowbirds in other areas of South America (Friedmann 1929, Friedmann et al. 1977, Salvador 1983). A second thrush nest was found with 2 cowbirds about to fledge. The experimental nestling (in the thrush nest) weighed 22.0 g at fledging, while the 2 nestlings at the other nest weighed 43.0 and 45.5 g.

Dietary suitability (Table 3) was judged by 3 criteria: species reported to successfully rear naturally placed eggs (Friedmann 1929, 1963; Friedmann et al. 1977; Fraga 1978; this study), species that feed young animal protein (Mason 1985), and the results of the cross-fostering experiments.

Nest survivorship.—Complete data on daily survivorship are in Mason (1985). Daily survivorship for the egg phase ranged from 0.988 (Rufous Hornero, $n = 15$ nests, 244 days of observation) to 0.852 (White-crested Tyrannulet, $n = 4$ nests, 27 days of observation). Daily survivorship for the nestling phase ranged from 0.996 (Rufous Hornero, $n = 13$ nests, 285 days of observation) to 0.857 (Fork-tailed Flycatcher, $n = 4$ nests, 28 days of observation).

The hornero's superior survivorship for both phases of the nesting cycle is largely attributable to its remarkable domed mud nest, which contributes to superior survivorship in other birds that also use it (Mason 1985). The difference between survivorship in hornero and mockingbird nests was significant for both phases of the nesting cycle (Table 4). Mockingbird survivorship exceeded that of the Rufous-

TABLE 3. Dietary suitability of different host species. Descriptions of food items can be found in Mason (1985). Cross-fostering experiments are discussed in Table 2 and text.

Host species	Natural successful rearing?	Animal protein provided?	Successful cross-fostering?
Rufous Hornero	Yes[a]	Yes	Yes?
Wren-like Rushbird		Yes	
Freckle-breasted Thornbird		Yes	
Firewood-gatherer	Yes[a]		Yes
Vermillion Flycatcher		Yes	Yes
Yellow-browed Tyrant	Yes[b]	Yes	Yes
Cattle Tyrant	Yes[a]		
Fork-tailed Flycatcher	Yes[a]		
Tropical Kingbird (*Tyrannus melancholicus*)	Yes[a]		
Great Kiskadee		Yes	Yes
White-rumped Swallow	Yes[b]		
House Wren	Yes[a,b]		
Chalk-browed Mockingbird	Yes[a,b]	Yes	
Rufous-bellied Thrush (*Turdus rufiventris*)	Yes[a,b]		
Creamy-bellied Thrush	Yes[b]		Yes?
Masked Gnatcatcher	Yes[a]		
Bay-winged Cowbird	Yes[a]	Yes	
Yellow-winged Blackbird (*Agelaius thilius*)	Yes[b]		
Blue-and-yellow Tanager	Yes[a]		
Saffron Finch	No[b]	No	No?
Grassland Yellow-Finch	No[a]	No	
Rufous-collared Sparrow	Yes[a,b]	Yes	
Hooded Siskin	Yes[a]		
House Sparrow	No[a]	Variable	No

[a] Records from literature (Friedmann 1929, 1963; Friedmann et al. 1977; Salvador 1983; Fraga 1985).
[b] Observations of this study.

collared Sparrow only for the nestling phase when all sources of mortality were considered. However, 13 mockingbird nest failures were attributed to pecking by Shiny Cowbirds, while only 1 such loss occurred at sparrow nests, and none occurred at nests of the hornero. When this source of mortality was removed, the daily survivorship of mockingbird nests improved significantly, surpassing that of the sparrow but remaining inferior to that of the hornero.

The product of the survivorship probabilities for the egg and nestling phases represents the probability of a nest fledging at least one young Shiny Cowbird under ideal conditions. The accepter species differed by almost an order of magnitude; when rejecters were considered, the difference was greater still (Table 5). Rejecters are included to show the success a female could experience were she to lay a mimetic egg. The Rufous Hornero, in the absence of rejection behavior, would be the best host choice. The best accepter species judged by survivorship (White-rumped Swallow) tended Shiny Cowbird fledgings more frequently than any other species (Table 6; Mason 1986).

DISCUSSION

Response to eggs.—The 26 species surveyed responded to 3 particular morphs of cowbird eggs in a species-typical fashion, with only 2 minor exceptions. This agrees with data from North America (Rothstein 1975a, b). In further agreement, rejection is almost always accomplished by ejection of the parasitic egg. Two species were classified as dual rejecters (Rufous Hornero, Fork-tailed Flycatcher) and one as a differential accepter favoring the spotted morph (Chalk-browed Mockingbird). Species that reject cowbird eggs are obviously unsuitable as hosts.

Desertion was infrequent, and egg burial was never observed. This also resembles most North American experiments in artificial parasitism

TABLE 4. Comparisons of daily mean survivorship rates. Numbers are presented as daily survivorship (SD, no. of nests surveyed, no. of observation days).

			z	$F(z)$	P
	Rufous Hornero vs. Chalk-browed Mockingbird				
Eggs	0.988 (0.007, 15, 244)	0.922 (0.012, 59, 477)	4.75	0.999+	<0.001, 1-tailed
Eggs[a]	0.988 (0.007, 15, 244)	0.950 (0.010, 59, 477)	3.11	0.999	=0.001, 1-tailed
Nestlings	0.996 (0.004, 13, 285)	0.953 (0.014, 28, 235)	2.95	0.998	=0.002, 1-tailed
	Chalk-browed Mockingbird vs. Chalk-browed Mockingbird[a]				
Eggs	0.922 (0.012, 59, 477)	0.950 (0.010, 59, 477)	1.79	0.963	=0.037, 1-tailed
	Chalk-browed Mockingbird vs. Rufous-collared Sparrow				
Eggs	0.922 (0.012, 59, 477)	0.899 (0.020, 45, 227)	0.99	0.839	=0.161, NS
Eggs[a]	0.950 (0.010, 59, 477)	0.903 (0.020, 45, 227)	2.10	0.982	=0.018, 1-tailed
Nestlings	0.953 (0.014, 28, 235)	0.901 (0.024, 26, 161)	1.87	0.969	=0.031, 1-tailed

[a] Nest failures due to pecking of eggs by Shiny Cowbirds eliminated from calculation of survivorship.

(Rothstein 1975a, b; but see Clark and Robertson 1981). Desertion may be a response to human presence or some disturbance at the nest other than the parasitic egg (Rothstein 1975a, 1976), but my techniques could not identify this possibility.

The species most likely to desert was the Rufous-collared Sparrow, which rejected only 3 of 18 artificially placed cowbird eggs, all by desertion. Fraga (1978) also found desertion to be infrequent. Hudson (1920) claimed that desertion was the typical response to parasitism in the Vermillion Flycatcher, but I observed acceptances in all 19 experiments.

Cowbird eggs incubated in nests of differential accepters fulfill the biological criterion for mimicry. Their resemblance to host eggs is adaptive and subject to selection. Human standards of similarity are misleading and inappropriate. For example, Chalk-browed Mockingbird eggs are easily distinguished (by humans) from spotted Shiny Cowbird eggs that are readily accepted. Three additional species are suspected of being differential accepters (Fraga 1985).

Nestling diet.—Cowbirds appear to require animal protein. Because most passerines feed their young arthropods (Hamilton and Orians 1965, Skutch 1976) and measures of overlap in nestling diets of sympatric species are typically high (Orians and Horn 1969, Anderson 1978, Maher 1979), cowbirds are probably little restricted in host choice by factors associated with nestling nutrition. This claim is supported by the large and taxonomically diverse list of species known to have reared Brown-headed (*M. ater*), Bronzed (*M. aeneus*), and Shiny cowbirds (Post and Wiley 1976, 1977; Friedmann et al. 1977).

Only 3 species (Saffron Finch, Grassland Yellow-Finch, Hooded Siskin) at my study sites are seed specialists. Neither finch is known to have reared cowbirds to fledging (Friedmann et al. 1977). Shiny Cowbird deaths in nests of the Grassland Yellow-Finch have been attributed to diet (Salvador 1983, Fraga 1985). Other seed specialists (*Carduelis* spp.) may augment the nestling diet with aphids, although reports are variable (Bent and collaborators 1968, Friedmann et al. 1977). Friedmann et al. (1977: 43) and Middleton (1977) observed Brown-headed Cowbirds to die in goldfinch nests.

The failure of a cross-fostered cowbird to survive in a nest of the House Sparrow is consistent with observations by Salvador (1983) and the lack of fledging records (Friedmann et al. 1977). Because seeds often form a substantial portion of the nestling diet, failures are probably due to dietary restriction rather than to discrimination against young cowbirds (Barrows 1889, Seel 1969, Anderson 1978, Eastzer et al. 1980).

Nest survivorship.—One source of nest failure was pecking by Shiny Cowbirds. Nests of highly preferred hosts are often multiply parasitized by several females (Fraga 1985; Mason 1980, 1986) and consequently subject to higher levels of pecking. This behavior depressed the success of Chalk-browed Mockingbird nests to a level not significantly different from that of the Rufous-collared Sparrow (Table 4). Pecking is sometimes less drastic, and cowbird eggs are occasionally lost during otherwise successful nesting attempts. Nonetheless, losses to peck-

TABLE 5. Survivorship estimates of Shiny Cowbirds in nests of different host species. Species with unsuitable nestling diets are not included.

	Survivorship		
	Eggs	Nestlings	Overall[a]
Rufous Hornero[b]	0.823 (15, 244)[c]	0.952 (13, 285)	0.783
Wren-like Rushbird	0.596 (20, 271)	0.715 (11, 126)	0.426
Tufted Tit-Spinetail	0.306 (4, 25)	1.000 (2, 31)	0.306
Freckle-breasted Thornbird	0.211 (7, 60)	0.746 (4, 48)	0.157
Firewood-gatherer	0.607 (11, 120)	0.671 (8, 106)	0.407
Vermillion Flycatcher	0.403 (22, 151)	0.405 (14, 143)	0.163
Yellow-browed Tyrant	0.713 (10, 95)	0.486 (8, 79)	0.347
Fork-tailed Flycatcher[b]	0.549 (7, 72)	0.117 (4, 28)	0.064
Great Kiskadee[d]	0.489 (7, 106)	0.481 (3, 39)	0.235
White-rumped Swallow	0.584 (9, 89)	0.819 (5, 70)	0.478
House Wren	0.273 (9, 44)	0.624 (3, 41)	0.170
Chalk-browed Mockingbird[e]	0.326 (59, 477)	0.514 (28, 235)	0.168
Rufous-bellied Thrush	0.370 (3, 30)	0.408 (2, 16)	0.151
Bay-winged Cowbird	0.190 (10, 82)	1.000 (2, 20)	0.190
Rufous-collared Sparrow	0.227 (45, 227)	0.233 (26, 161)	0.053

[a] Overall survivorship = (egg survivorship) × (nestling survivorship).
[b] Rejects cowbird eggs.
[c] Mean survivorship (no. of nests surveyed, no. of observation days).
[d] Response to spotted eggs uncertain (Mason 1986).
[e] Rejects immaculate cowbird eggs.

ing are density-dependent forms of mortality because they are inflicted by cowbirds

The survivorship probabilities (Table 5) represent the freedom of nests from complete loss, and estimate the success of cowbirds under ideal circumstances. Differential mortality of cowbirds within a nest will lower success below rated survivorship. Competition among nestlings for the limited food available can introduce differential mortality as in adaptive brood reduction (Lack 1954): competition is size and age mediated, and inequalities in competitive ability are introduced by the amount of food supplied, size at hatching, magnitude of hatching asynchrony, and normal nestling growth rate.

Successful parasitism requires that female cowbirds properly synchronize their laying with that of the host. Eggs laid late may fail to hatch, or hatch so late that the nestling will be competitively inferior. The extremely low fledging weight of the cowbird nestling in the nest of the Creamy-bellied Thrush and the death of the cowbird nestling cross-fostered in a nest of the Rufous Hornero are illustrative (Table 2).

The life-history characteristics of some species suggest that severe nestling competition may be difficult to avoid. The advantage of the cowbird's shorter incubation period is offset by the Chalk-browed Mockingbird's larger size at hatching and faster growth rate (Fraga 1985, Mason 1985). I observed only 1 case of starvation among 16 cowbird nestlings in 10 broods, but Fraga (1985) reported 12 such cases among 20 nestlings from 15 nests. The reasons for increased starvation at Fraga's site are unknown.

Competition between host and parasite is unlikely to adversely affect cowbirds in nests of the Rufous-collared Sparrow. Nestling sparrows are smaller at hatching and grow more slowly (King 1973, Fraga 1978, Mason 1985). Fraga (1985) found that the overall success of naturally laid cowbird eggs in Rufous-collared Sparrow nests was 0.056 (vs. 0.053 in Table 4). On the other hand, competition is likely if sparrow nests are multiply parasitized. The nutritional demands of two cowbird young probably exceed the capabilities of that host to rear two healthy cowbirds. Fraga (1978, 1983b, 1985) reported no cases of sparrows fledging two cowbirds, while King (1973) showed that growth rate and fledging weight were both reduced when two cowbird nestlings were in the nest. In the region of South America studied, multiple parasitism is almost entirely restricted to large, highly preferred hosts; smaller hosts (like the sparrow) are slightly used (Mason 1986).

Friedmann (1963) pointed out that the suc-

TABLE 6. Observations of host species attending Shiny Cowbird fledglings.

Host species	Date of observation
White-rumped Swallow (7 nests)	
1	14 Nov 1978, 18 Nov 1978
2	24 Nov 1978, 30 Nov 1978
3	27 Nov 1978, 28 Nov 1978
4	8 Dec 1978, 12 Dec 1978
5	9 Dec 1978, 14 Dec 1978
6	19 Dec 1978
7	23 Dec 1978
House Wren	22 Nov 1978
Yellow-winged Blackbird	12 Jan 1979
Masked Gnatcatcher	2 Feb 1979

cess of cowbirds is characteristically less than that of their hosts. Three important sources of mortality (diet, density-dependent egg pecking, and the adverse affect of intranest competition) are probably the main reasons for this observation.

Host quality is sensitive to the natural-history attributes of nesting species and to cowbird behavior. Some adaptations of cowbirds can circumvent apparent barriers to successful parasitism. Egg rejection can be overcome by mimicry, as has been documented for the Chalk-browed Mockingbird (Fraga 1985, this study). The Rufous Hornero is apparently a frequent host in other parts of Argentina (Friedmann 1929, Friedmann et al. 1977, Salvador 1983), despite its status as a rejecter in Buenos Aires Province. In the case of large hosts, the shorter the host incubation period, the more likely cowbird nestlings will experience severe competition. Egg pecking may reduce nestling competition by selectively destroying host eggs, whose numbers vary inversely with those of the cowbird in Chalk-browed Mockingbird nests (Mason 1980, Fraga 1985). However, entire clutches are often destroyed, thus increasing the relative value of other species. A generalized pattern of resource use results from the Shiny Cowbird's ability to exploit several avenues of adaptive niche expansion.

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