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SHINY COWBIRD PARASITISM IN TWO AVIAN COMMUNITIES IN PUERTO RICO

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ABSTRACT.—The Shiny Cowbird (*Molothrus bonariensis*), a brood parasite, has recently expanded its range from South America to Puerto Rico via the Lesser Antilles. This species is a host generalist and, on reaching Puerto Rico, encountered avian species with no history of social parasitism. In mangrove habitat study areas, 42% of the resident non-raptorial land bird species were parasitized. Some species were heavily parasitized; e.g., Yellow Warbler (*Dendroica petechia*)—76% of nests parasitized, Black-whiskered Vireo (*Vireo altiloquus*)—82%, Puerto Rican Flycatcher (*Myiarchus antillarum*)—85%, Yellow-shouldered Blackbird (*Agelaius xanthomus*)—95%, Troupial (*Icterus icterus*)—100%, Black-cowled Oriole (*I. dominicensis*)—100%. Others suffered low rates of parasitism (2 to 17% of nests examined); e.g., Gray Kingbird (*Tyrannus dominicensis*), Red-legged Thrush (*Turdus plumbeus*), Bronze Mannikin (*Lonchura cucullata*), Northern Mockingbird (*Mimus polyglottos*), Greater Antillean Grackle (*Quiscalus niger*). Cowbird parasitism affected hosts by (1) depressing nest success an average of 41% below non-parasitized nests, and (2) reducing host productivity. Parasitized host nests hatched 12% fewer eggs and fledged 67% fewer of their own chicks than non-parasitized pairs.

In contrast to the host specialization shown by most other parasites, some species of cowbirds spread the burden of parasitism among many species. This habit reduces selective pressures that favor the host's development of counter-adaptive responses against the parasite, and makes more foster parents available to the cowbird. A nonspecific parasite need not be regarded as primitive or unable to specialize, because remaining a generalist may be an important adaptation in itself, allowing opportunistic exploitation of many species encountered by the parasite (Gochfeld 1979). The abundance and expansion of both the Brown-headed Cowbird (*Molothrus ater*; Mayfield 1965, Rothstein et al. 1980) and the Shiny Cowbird (*M. bonariensis*; Post and Wiley 1977a) show that generalist habits can be successful.

Although a generalist habit may enable host populations to maintain parasitic loads more easily (reviewed in Payne 1977), some cowbird populations have had extreme depressive effects on the reproductive success of certain host species (e.g., Brown-headed Cowbird on Kirtland's Warbler, *Dendroica kirtlandii*, Mayfield 1972, Walkinshaw 1983; Shiny Cowbird on

Rufous-collared Sparrow, *Zonotrichia capensis*, in Argentina, King 1973, Fraga 1978; on Yellow Warbler, *Dendroica petechia*, in Barbados, Bond 1966; and on Yellow-shouldered Blackbird, *Agelaius xanthomus*, in Puerto Rico, Post and Wiley 1976, 1977b).

Most cowbird research has been conducted in areas where the parasites have long coexisted with host populations. During this long coexistence, cowbird and host populations have coevolved patterns of exploitation and avoidance, some of which are specialized enough to obscure their origin or possible evolutionary route. The Shiny Cowbird reached Puerto Rico by "island hopping" (perhaps aided by introductions on some islands) through the Lesser Antilles from South America and Trinidad (Post and Wiley 1977a). Although the cowbird was first recorded at the northeasternmost part of the island in 1955 (Grayce 1957), there is strong circumstantial evidence that the species arrived before that time (Post and Wiley 1977a). In 1963, Biaggi (1970) saw more than 200 cowbirds at Yabucoa, southeastern Puerto Rico. M. Gochfeld (Buckley and Buckley 1970) found 250 near the Guajataca cliffs in northwestern Puerto Rico in 1965. It is not known

when cowbirds reached southwestern Puerto Rico, but it is likely that they spread westward through the island and arrived there somewhat later.

The study of the Shiny Cowbird and its recently-parasitized host populations in the West Indies offers a unique opportunity to examine the biology of brood parasitism early in the history of interaction between a generalist parasite and a naïve local avifauna. In a seven-year study, I investigated the relationships between Shiny Cowbirds and their hosts in Puerto Rico with three objectives in mind: (1) to determine the effects of Shiny Cowbird parasitism on an avian community at the frontier of the parasite's expanding range, (2) to examine factors critical to selection of hosts by the Shiny Cowbird, and (3) to determine if nesting birds at this frontier, presumably inexperienced with social parasitism, had anti-parasite habits and, if so, the origins of these patterns. Here I will present data that show the extent and effect of brood parasitism on avian communities which have recently encountered the Shiny Cowbird.

Because the cowbirds and the resident avian community have recently met, I predicted that the incidence of parasitism would be high owing to the naïveté of nesting birds to this form of exploitation. Since brood parasitism has been shown to depress host productivity in systems where host and parasite have a longer history of coexistence (Payne 1977), I expected host nest success and productivity at parasitized nests in Puerto Rico would be lower than in non-parasitized nests.

STUDY AREAS

I studied brood parasitism in mangrove habitats at Roosevelt Roads Naval Station at the easternmost point of Puerto Rico, and at Boquerón Forest in southwestern Puerto Rico. The Roosevelt Roads study area is about 60 km east of San Juan. Ewel and Whitmore (1973) included the 3,260-ha naval station within the Subtropical Dry Forest Zone. Annual rainfall averages 162 cm, with most rain falling in two periods: May, and August through November (data from Fajardo Station, 6 km west of Roosevelt Roads). Mean annual temperature is 25.9°C (1975–1981).

Mangrove forest dominates the extensive tidal lands and occupies about 25% (814 ha) of the station's land area. The remainder contains level, alluvial valleys and low hills (less than 150 m above sea level) which are vegetated with grasses, various scrubs, and intermediate successional stages. Military installations and housing/recreation complexes occupy a considerable portion of the station.

Buell and Dansereau (1966) have described the vegetative structure of Roosevelt Roads.

Because I wanted to restrict my work to a vegetatively simple ecosystem, I chose to conduct the research within the mangrove forests. This also made comparisons between the southwestern and eastern study areas more equitable because the forests are composed of the same dominant species, although structure differs somewhat.

At Roosevelt Roads, the forest is composed of four mangrove species: black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), button mangrove (*Conocarpus erectus*), and red mangrove (*Rhizophora mangle*). *Rhizophora* is nearest the sea and *Laguncularia* and *Conocarpus* farthest inland. Inner mangrove areas with sandy soils are often characterized by a saltwort (*Batis maritima*)-*Avicennia* scrub and glasswort (*Salicornia*) or sea-purslane (*Sesuvium portulacastrum*) mat. The prevalent vegetation type in the elevated areas surrounding the mangroves is thicket dominated by the introduced leadtree *Leucaena leucocephala*. Open hillsides and abandoned pastureland characteristically are covered with graminoids, especially guinea grass (*Panicum maximum*).

As is true throughout coastal Puerto Rico, the Roosevelt Roads mangrove forests have been extensively disturbed (Buell and Dansereau 1966), although the resulting salt flats, scrub, and savannas are now returning to forests. Some mangroves served as depositories for soil removed from graded uplands. Dredge material from the harbor and access channels was deposited on mangroves or on areas seaward of existing land. These have revegetated primarily with *Avicennia*. One such fill ("LT") served as one of my two study sites at Roosevelt Roads. The other main site ("OC") was a less disturbed, older mixed-mangrove forest.

The southwestern coastal study site lies between Bahía Sucia and Bahía Montalva, but primarily within the Commonwealth Boquerón Forest. Ewel and Whitmore (1973) also characterized this area as within the Subtropical Dry Forest Zone although, at a mean of 68 cm, annual precipitation is less than half that at Roosevelt Roads. Like the eastern study area, most rainfall occurs in two periods: May, and August through November. Mean annual temperature (1975–1980) is 26.8°C.

The Boquerón Forest study area consists of a red mangrove fringe (approximately 25% of the area; Puerto Rico Department of Natural Resources 1976), black mangrove (about 55%), and salt flats (10%). I inspected the other main association (salt spray exposed sandy beach thicket) irregularly. The mangrove forests con-

sist of old, tall, red and black mangrove stands as well as re-vegetating salinas. In contrast to Roosevelt Roads, there are many offshore mangrove cays, which I visited regularly to check nests. Inland from the mangrove, the dry hillside and alluvial fall is characterized by an oxborn bucida (*Bucida buceras*)-mesquite (*Prosopis juliflora*) savanna/woodland or gumbo-limbo (*Bursera simaruba*) savanna/woodland, with dense epiphytic ball moss (*Tillandsia recurvata*) throughout.

METHODS

Data presented here were collected between 1975 and 1981. My schedule of data collection at Roosevelt Roads was as follows: 1975—study area visited at least every other day throughout the breeding season (March–June), biweekly visits were made during the non-breeding season; 1976—area visited at least on alternate days from July through August; 1977–1978—daily or alternate day visits through breeding season, biweekly visits during non-breeding season; 1979–1981—at least every other day visits through breeding season, except July 1980 when data were collected twice per week, non-breeding season visits at weekly or biweekly intervals.

My schedule of visits to the southwestern study area was: 1977 through 1979—data collected at least once per week during the breeding season, study area visited irregularly during non-breeding season; 1980—weekly visits from April through June, and August, with daily visits during July, irregular visits during non-breeding season.

I concentrated on three of the most common nesting species in each study area: Yellow-shouldered Blackbird, Yellow Warbler, and Greater Antillean Grackle (*Quiscalus niger*).

I found nests by regularly searching the study areas. The site of each nest was marked with a coded tag (unobtrusively placed), and nest locations were plotted on field maps. Distances and compass directions between active nests were measured and plotted. At each visit to the study areas, I inspected nests to determine number of host and, if present, parasite eggs and chicks. I inconspicuously marked all eggs with indelible ink; some were measured and weighed. Weights were taken using Pesola spring scales of 5-g and 10-g capacities. Measurements were made to the nearest 0.1 mm. I routinely checked eggs for damage. Hatchlings were identified from their nestmates by food dye (blue, green, yellow, orange) on an inconspicuous part of the body (e.g., under wing). When chicks were old enough, I banded them with three colored celluloid leg bands in unique combinations.

Some nests were manipulated, either for experiments or to reduce cowbird loads (e.g., cowbird egg removal). I did not include these manipulated nests in analyses that would be biased by such experiments (e.g., nest success, hatchability, fledging success), but several were used in calculating percentage of host nests parasitized and mean clutch sizes.

I attempted to determine the cause(s) of nest failure for 19 species of birds and for parasitized species, and compared failure rates between parasitized and non-parasitized nests to determine if differences existed. Some losses were clearly the result of predation: e.g., rat-chewed eggs or chicks. Nests where chicks or eggs cleanly disappeared were assumed to have been plundered (usually by Pearly-eyed Thrashers, *Margarops fuscatus*). Disappearance of chicks or eggs from damaged nests was attributed to black rat (*Rattus rattus*) predation. Exposure was thought to be responsible for death of chicks found in or under nests after a storm where I found no sign of predation or arthropod infestation. Nests where activity had ceased before egg-laying or where the adults no longer tended their eggs were classed as deserted. Eggs at some deserted nests may have been subsequently eaten by predators, which perhaps led to an underestimate of desertion and overestimate of predation rates. Nest failures due to nest mites or ants were occasionally noted. Warble fly (*Neomusca [Philornis] pici*) larva infestation caused the loss of some chicks.

I defined a nest as "active" when the resident laid at least one egg or, if parasitized and no host egg was laid, the host incubated the cowbird egg(s). Nests where building occurred but no eggs (host or parasite) were laid were not included in calculations of nesting effort. A nest from which one or more chicks fledged (either host or parasite) was considered successful.

I followed statistical methods of Hollander and Wolfe (1973) and Zar (1975). Significance level was set at 0.05. When the underlying assumptions (e.g., normality, equal variance) were not violated, or only slightly so, I used parametric statistical methods to test for sample differences. In other cases, I applied non-parametric statistics.

RESULTS

PARASITISM RATES

One or more parasitized nests were encountered for 42% (11/26) of the non-raptorial land bird species breeding on the two study areas. At Roosevelt Roads, regular nest inspections of 17 bird species ($n = 823$ nests) revealed cowbird parasitism of eight species (47%; Ta-

ble 1). Prevalence of parasitism for these species ranged from 2 to 100%. Within this wide range, I found two distinct groups: Gray Kingbirds (*Tyrannus dominicensis*), Red-legged Thrushes (*Turdus plumbeus*), Greater Antillean Grackles, and Bronze Mannikins (*Lonchura cucullata*) had a low rate of nest parasitism ranging from 2 to 17%, and the remaining four species, Yellow Warbler, Black-whiskered Vireo (*Vireo altiloquus*), Yellow-shouldered Blackbird, and Black-cowled Oriole (*Icterus dominicensis*), had a high rate of parasitism, from 75 to 100% of nests examined. An average of 1.1 ± 0.02 [SE] (range 1–2) cowbird eggs were laid per parasitized nest in the species incurring low parasitism rates. The mean number of cowbird eggs in nests of regularly-parasitized species was significantly greater at 2.7 ± 0.24 (range 1–8; $P < 0.05$, Mann-Whitney test) than in nests of irregularly-parasitized species.

Five of the seven (71%) species monitored at Boquerón Forest were parasitized at levels ranging from 8 to 100% of nests observed ($n = 154$ nests; Table 2). The Northern Mockingbird (*Mimus polyglottos*), a species for which I found no parasitized nests at Roosevelt Roads, incurred a low rate of parasitism (8%) at Boquerón. The other four parasitized species (Yellow Warbler; Puerto Rican Flycatcher, *Myiarchus antillarum*; Yellow-shouldered Blackbird; Troupial, *Icterus icterus*) were regularly parasitized (mean percentage of nests parasitized = 88.5%, range = 80–100%). I found no parasitized Gray Kingbird nests in the southwestern study area. Adelaide's Warbler (*Dendroica adelaidae*) did not nest on the study area, but I found parasitized nests in the foothills adjacent to the mangroves. An average of 3.0 ± 0.05 cowbird eggs per parasitized nest (range 1–8) were laid in the nests of regularly-parasitized species. The single parasitized Northern Mockingbird nest contained one cowbird egg.

The same two-group pattern of parasitism incidence was evident among the collective breeding populations of parasitized species (681 nests; $n = 11$ species) of both study areas. Regularly-parasitized species hatched more cowbird eggs ($\bar{x} = 1.1 \pm 0.10$ per nest; $n = 6$ species) and fledged more cowbird young ($\bar{x} = 0.6 \pm 0.13$) than species where cowbird parasitism was only occasional (\bar{x} hatched = 0.02 ± 0.08 , \bar{x} fledged = 0.01 ± 0.02 ; $n = 5$ species; both $P < 0.001$; Fisher-Behrens t -test).

FINAL CLUTCH SIZE

In both study areas host clutch sizes were consistently smaller (average –12%) in parasitized nests than non-parasitized nests, except

for Red-legged Thrushes, grackles, and Yellow-shouldered Blackbirds at Boquerón Forest, and the single parasitized Northern Mockingbird nest at Boquerón (Mann-Whitney test, 1-tailed; Table 3).

For some parasitized species or localities, the number of cowbird eggs per nest was greater than the number of host eggs. The mean number of cowbird eggs exceeded the mean number of host eggs at nests of the Yellow-shouldered Blackbird (21% more cowbird than host eggs), both at Roosevelt Roads (3.22 vs. 2.63; $P < 0.01$) and Boquerón Forest (3.08 vs. 2.62; $P = 0.025$, Mann-Whitney test, 1-tailed). This occurred also for the Puerto Rican Flycatcher (+9%: 3.18 vs. 2.91; $P > 0.05$), Black-whiskered Vireo (+15%: 2.56 vs. 2.22; $P > 0.05$), and Black-cowled Oriole (+89%: 3.92 vs. 2.07; $P < 0.0025$), and Yellow Warbler (+47%: 2.94 vs. 2.00; $P = 0.025$) at Boquerón. In contrast, host eggs outnumbered cowbird eggs at Greater Antillean Grackle (+173%: 3.09 vs. 1.13; $P = 0.025$) and Troupial (+50%: 2.40 vs. 1.60; $P > 0.05$) nests, and Yellow Warbler (+27%: 2.07 vs. 1.63; $P < 0.025$) nests at Roosevelt Roads.

Parasitized nests received from one to eight cowbird eggs. For some species, the mean total number of eggs per nest (i.e., host + cowbird eggs) was greater than the average clutch size at unparasitized nests: Yellow Warbler at Roosevelt Roads—3.6 eggs at parasitized nests vs. 2.6 at non-parasitized nests ($P = 0.025$, Mann-Whitney 2 sample test, 1-tailed); Yellow Warbler at Boquerón Forest—4.8 vs. 2.8 ($P = 0.05$); Yellow-shouldered Blackbird at Roosevelt Roads—5.7 vs. 3.0 ($P = 0.025$); Yellow-shouldered Blackbird at Boquerón Forest—5.6 vs. 2.5 ($P = 0.05$); Greater Antillean Grackle—4.2 vs. 3.2 ($P < 0.05$). Although not statistically significant, the total number of eggs in parasitized nests was greater than that in unparasitized nests of Puerto Rican Flycatchers (6.1 vs. 4.5) and Black-whiskered Vireos (4.8 vs. 3.0). The addition of cowbird eggs increased the number of eggs in parasitized nests 31% (grackle) to 124% (blackbirds at Boquerón) above non-parasitized clutch sizes (\bar{x} for five species = 65%).

For most parasitized species, there was a strong negative relationship between the number of cowbird eggs deposited in nests and the number of host eggs laid. Only grackles (r [product moment correlation coefficient] = 0.57; $0.05 < P < 0.10$), Black-whiskered Vireos ($r = -0.11$; $0.10 < P < 0.20$), and the Yellow-shouldered Blackbird ($r = 0.57$; $0.10 < P < 0.20$) population at Boquerón Forest did not show this relationship. Regularly-parasitized species experienced an average reduction

TABLE 1. Summary of breeding bird nest success, productivity, and degree of parasitism by the Shiny Cowbird at Roosevelt Roads Naval Station, Puerto Rico, 1975-1981.

Component	Species*																
	MC	GtC	CE	GKb	RIT	Mb	PeT	BwV	YW	BQ	SHT	BFGq	YsBb	GAG	BcO	BM	NM
Total no. active nests	5	29	14	61	25	31	57	11	87	68	17	22	98	218	12	6	62
No. successful nests	4	18	7	45	12	16	35	7	35	24	8	6	37	138	10	4	34
(%)	(80)	(62)	(50)	(74)	(48)	(52)	(61)	(64)	(40)	(35)	(47)	(27)	(38)	(63)	(83)	(67)	(55)
No. host eggs	14	57	37	171	75	91	167	26	176	179	50	65	248	689	29	32	382
Mean host clutch size	2.8	2.0	2.6	2.8	3.0	2.9	2.9	2.4	2.1	2.6	2.9	3.0	2.5	3.2	2.4	5.3	6.2
No. host eggs hatch	8	37	17	130	46	54	101	13	52	73	29	20	48	404	13	21	203
(% of eggs)	(57)	(65)	(46)	(76)	(61)	(59)	(60)	(50)	(30)	(41)	(58)	(31)	(19)	(59)	(45)	(66)	(53)
No. host young fledged	8	31	11	101	29	40	75	7	19	50	18	14	12	323	4	20	170
(% of eggs)	(57)	(54)	(30)	(59)	(39)	(44)	(45)	(27)	(11)	(28)	(36)	(22)	(5)	(47)	(14)	(63)	(45)
No. fledged/active nest	1.6	1.1	0.8	1.7	1.2	1.3	1.3	0.6	0.2	0.7	1.1	0.6	0.1	1.5	0.3	3.3	2.7
No. fledged/successful nest	1.6	1.7	1.6	2.2	2.4	2.5	2.1	1.0	0.5	2.1	2.3	2.3	0.3	2.3	0.4	5.0	5.0
No. nests parasitized	0	0	0	1	1	0	0	9	65	0	0	0	93	23	12	1	0
(% of nests)	(0)	(0)	(0)	(2)	(4)	(0)	(0)	(82)	(75)	(0)	(0)	(0)	(95)	(11)	(100)	(17)	(0)
Success of parasitized nests				0.0	0.0	0.5	0.6	0.6	0.5	0.5	0.7	0.3	0.2	0.7	0.8	0.0	0.6
Success of nests not parasitized	0.8	0.6	0.5	0.8	0.5	0.5	0.6	1.0	0.2	0.4	0.7	0.3	0.2	0.7	0.8	0.8	0.6
No. cowbird eggs				1	1	1	23	23	106				299	26	47	1	
Mean no. cowbird eggs/parasitized nest				1.0	1.0		2.6	2.6	1.6				3.2	1.1	3.9	1.0	
No. cowbird eggs hatched				0	0		11	11	57				81	4	37	0	
(% of eggs)				(0)	(0)		(48)	(48)	(54)				(27)	(15)	(79)	(0)	0
No. cowbirds fledged				0	0		8	8	32				55	2	36	0	(0)
(% of eggs)				(0)	(0)		(35)	(35)	(30)				(18)	(8)	(77)	(0)	0
No. cowbirds fledged/active nest				0	0		0.7	0.7	0.4				0.6	0.01	3.0	0	0
No. cowbirds fledged/successful nest				0	0		1.1	1.1	0.9				1.5	0.01	3.6	0	0

* Common names: MC = Mangrove Cuckoo, GtC = Green-throated Carib, CE = Caribbean Elaenia, GKb = Gray Kingbird, RIT = Red-legged Thrush, Mb = Northern Mockingbird, PeT = Pearly-eyed Thrasher, BwV = Black-whiskered Vireo, YW = Yellow Warbler, BQ = Bananaquit, SHT = Stripe-headed Tanager, BFGq = Black-faced Grassquit, YsBb = Yellow-shouldered Blackbird, GAG = Greater Antillean Grackle, BcO = Black-cowbird Oriole, BM = Bronze Mannikin, NM = Nutmeg Mannikin.

TABLE 2. Summary of breeding bird nest success, productivity, and degree of parasitism by the Shiny Cowbird at Boquerón Forest, southwestern Puerto Rico, 1977–1980.

Component	Species*						
	PRF	GKb	Mb	YW	BQ	YsBb	Tr
Total no. active nests	13	15	13	20	22	66	5
No. successful nests	9	11	9	9	10	26	4
(%)	(69)	(73)	(69)	(45)	(45)	(39)	(80)
No. host eggs	41	43	38	41	55	163	12
Mean host clutch size	3.2	2.9	2.9	2.1	2.5	1.5	2.4
No. host eggs hatch	22	38	28	14	27	60	7
(% of eggs)	(54)	(88)	(74)	(34)	(49)	(37)	(58)
No. host young fledged	13	28	24	7	18	30	4
(% of eggs)	(32)	(65)	(63)	(17)	(33)	(18)	(33)
No. fledged/active nest	1.0	1.9	1.8	0.4	0.8	0.5	0.8
No. fledged/successful nest	1.4	2.5	2.7	0.8	1.8	1.2	1.0
No. nests parasitized	11	0	1	16	0	59	5
(% of nests)	(85)	(0)	(8)	(80)	(0)	(89)	(100)
Success of parasitized nests	0.6		1.0	0.4		0.4	0.8
Success of nests not parasitized	1.0	0.7	0.7	0.8	0.5	0.1	
No. cowbird eggs	35		1	47		182	8
Mean no. cowbird eggs/parasitized nests	3.2		1.0	2.9		3.1	1.6
No. cowbird eggs hatched	13		1	14		69	7
(% of eggs)	(37)		(100)	(30)		(38)	(88)
No. cowbirds fledged	11		0	7		42	6
(% of eggs)	(31)		(0)	(15)		(23)	(75)
No. cowbirds fledged/active nest	0.8		0	0.4		0.6	1.2
No. cowbirds fledged/successful nest	1.2		0	0.8		1.6	1.5

* Common names: PRF = Puerto Rican Flycatcher, GKb = Gray Kingbird, Mb = Northern Mockingbird, YW = Yellow Warbler, BQ = Bananaquit, YsBb = Yellow-shouldered Blackbird, Tr = Troupial.

of host eggs ranging from 13% (nests with only one cowbird egg added) below mean clutch size at unparasitized nests to 74% at nests with the maximum observed number of cowbird eggs (eight at three Yellow-shouldered Blackbird nests). Correlation coefficients for these species were as follows: Puerto Rican Flycatcher— -0.97 ($P < 0.01$; Null hypothesis = 0; t -test for correlation, 2-tailed); Yellow Warbler— -0.99 (Roosevelt Roads; $P < 0.02$) and -0.94 (Boquerón Forest; $P < 0.01$); Troupial— -1.0 ($P < 0.001$); Yellow-shouldered Blackbird— -0.88 (Roosevelt Roads; $P < 0.002$); Black-cowled Oriole— -0.82 ($P < 0.05$).

HATCHING SUCCESS

Fewer host eggs hatched in parasitized nests than in non-parasitized nests of vireos, Puerto Rican Flycatchers, and the Boquerón populations of the warbler (Table 3). Numbers of host chicks were no different between parasitized and non-parasitized blackbird, grackle, and warbler nests at Roosevelt Roads. Parasitized blackbirds at Boquerón Forest hatched more host chicks than did non-parasitized pairs.

NEST SUCCESS

Host nest success at the Roosevelt Roads study area was generally greater at non-parasitized nests than at parasitized nests (Tables 1 and

2); nest success at non-parasitized nests (nine species) averaged 41% above that at parasitized nests. Examined collectively, nest success of parasitized pairs was less than that of non-parasitized pairs for the 11 species on both study areas ($P < 0.001$, Kolmogorov-Smirnov test). The single parasitized nests of the Red-legged Thrush, Bronze Mannikin, and Gray Kingbird all failed, whereas the only Northern Mockingbird nest parasitized fledged young (although the cowbird chick did not fledge). Nevertheless, some host species populations had no better nest success at non-parasitized nests than at parasitized nests; i.e., Yellow Warblers at Roosevelt Roads, Yellow-shouldered Blackbirds at Roosevelt Roads and Boquerón Forests ($P > 0.05$, Tables 1 and 2).

On the average, parasitized pairs fledged 67% fewer host chicks than non-parasitized pairs (0.5 host chicks/nest vs. 1.5 chicks/nest at non-parasitized nests for five species), although only Puerto Rican Flycatchers, vireos, and the warbler population at Boquerón showed significant differences (Table 3). Parasitized hosts (six species) fledged an average of 2.4 times as many cowbird chicks as host chicks. Only grackles fledged more host chicks (1.36 ± 0.28 /nest) than cowbird chicks (0.09 ± 0.06 ; $P < 0.05$, Mann-Whitney 2 sample test, 2-tailed) at parasitized nests. Other species fledged more cowbirds than host chicks: Puerto Rican Flycatch-

ers— 1.00 ± 0.36 vs. 0.64 ± 0.39 ($P < 0.02$); Black-whiskered Vireos— 0.89 ± 0.31 vs. 0.33 ± 0.02 ($P < 0.02$); Yellow Warblers (Roosevelt Roads)— 0.49 ± 0.14 vs. 0.17 ± 0.06 ($P < 0.001$), (Boquerón Forest)— 0.44 ± 0.16 vs. 0.0 ($P < 0.001$); Black-cowled Orioles— 3.00 ± 0.48 vs. 0.33 ± 0.14 ($P < 0.0005$); and the Yellow-shouldered Blackbird (Roosevelt Roads)— 0.59 ± 0.09 vs. 0.11 ± 0.04 ($P < 0.02$), (Boquerón Forest)— 0.71 ± 0.14 vs. 0.47 ± 0.11 ($P > 0.05$); and Troupial— 1.20 ± 0.38 vs. 0.80 ± 0.38 ($P > 0.05$).

Although the total number of eggs resulting from cowbird eggs being added to the host's clutch was characteristically greater than the mean unparasitized clutch, the number of chicks (cowbird + host) fledged from parasitized nests generally did not differ from non-parasitized nests. More chicks (cowbird + host) fledged from parasitized nests than non-parasitized nests only for the blackbird (1.14 ± 0.21 vs. 0.29 ± 0.29 ; $P < 0.001$, Mann-Whitney 2-sample test, 2-tailed) population at Boquerón. The Boquerón Yellow Warbler population fledged fewer chicks (host + cowbird) at parasitized nests (0.44 ± 0.16) than at non-parasitized nests (1.75 ± 0.63 ; $P < 0.02$). Other populations or species had the following mean numbers of chicks (host + cowbird chicks at parasitized nests vs. host chicks at nonparasitized nests) fledge: Puerto Rican Flycatcher— 1.64 ± 0.43 vs. 3.00 ± 0.0 , Black-whiskered Vireo— 1.22 ± 0.43 vs. 2.00 ± 0.0 , Yellow Warbler (Roosevelt Roads)— 0.67 ± 0.11 vs. 0.36 ± 0.16 , Yellow-shouldered Blackbird (Roosevelt Roads)— 0.70 ± 0.10 vs. 0.40 ± 0.40 , Greater Antillean Grackle— 1.45 ± 0.27 vs. 1.48 ± 0.09 (all $P > 0.05$).

Forty-seven percent of the 977 nests (19 species) failed and these failures were attributed to the following: 61% to predation ($n = 282$), 33% to desertion (150), 1% to exposure (5), <1% to warble fly parasitism (2), <1% to nest falls (1), 1% to arthropod (ant and mite) infestations (3), 4% to unknown causes (18). Overall, non-parasitized nests were preyed on more often than parasitized nests (\bar{x} for five species = 23.4% for non-parasitized nests vs. 13.5% for parasitized nests). Of the five parasitized species (blackbird, flycatcher, vireo, warbler, grackle) for which analyses could be made, only the Yellow-shouldered Blackbird population at Roosevelt Roads experienced greater predation rates at parasitized nests than at non-parasitized nests ($P < 0.05$; Kolmogorov-Smirnov 2-sample test, 2-tailed).

HOST DESERTION

The average desertion rate for these five parasitized species was higher at parasitized nests

TABLE 3. Comparison of clutch size, hatching success, and fledging success at parasitized and non-parasitized nests of 10 host species at Roosevelt Roads Naval Station and Boquerón Forest study areas, Puerto Rico, 1975–1981.

Locality	Species ^b	Mean number per nest for hosts											
		Eggs				Eggs hatched				Chicks fledged			
		Parasitized		Non-parasitized		Parasitized		Non-parasitized		Parasitized		Non-parasitized	
Roosevelt Roads	RIT	1	3.00	24	3.00 ± 0.10	1	0	24	1.92 ± 0.29	1	0	24	1.21 ± 0.27
	BwV	9	2.22 ± 0.28	2	3.00 ± 0.00***	9	0.89 ± 0.31	2	2.50 ± 0.50*	9	0.33 ± 0.02	2	2.00 ± 0.00**
	YW	46	2.07 ± 0.12	11	2.55 ± 0.21***	65	0.49 ± 0.10	22	0.91 ± 0.25	65	0.17 ± 0.06	22	0.36 ± 0.16
	YsBb	54	2.63 ± 0.13	4	3.00 ± 0.23***	93	0.49 ± 0.08	5	0.40 ± 0.40	93	0.11 ± 0.04	5	0.40 ± 0.40
	GAG	23	3.09 ± 0.12	195	3.17 ± 0.06	22	1.86 ± 0.30	195	1.94 ± 0.10	22	1.36 ± 0.28	195	1.48 ± 0.09
	BcO	14	2.07 ± 0.29	0		12	1.08 ± 0.23	0		12	0.33 ± 0.14	0	
Boquerón Forest	BM	1	5.00	5	5.40 ± 0.25	1	0	5	4.20 ± 1.07	1	0	5	4.00 ± 1.00
	PRF	11	2.91 ± 0.21	2	4.50 ± 0.50**	11	1.36 ± 0.43	2	3.50 ± 0.50*	11	0.64 ± 0.39	2	3.00 ± 0.0*
	Mb	1	3.00 ± 0.00	12	2.92 ± 0.08	1	3.00	12	2.08 ± 0.38	1	0	12	1.75 ± 0.39
	YW	8	2.00 ± 0.29	4	2.75 ± 0.25*	16	0.19 ± 0.10	4	2.75 ± 0.25**	16	0	4	1.75 ± 0.63***
	YsBb	39	2.62 ± 0.15	6	2.50 ± 0.20	7	0.98 ± 0.42	7	0.29 ± 0.29**	59	0.47 ± 0.11	7	0.29 ± 0.29
	Tr	5	2.40 ± 0.40	0		5	1.40 ± 0.51	0		5	0.80 ± 0.38	0	

* Only nests with complete clutches are included in calculations for number of host eggs per nest. Data for hatching and fledging are from non-manipulated nests and nests where hosts laid at least one egg. Probability levels: * = $P < 0.05$, ** = $P < 0.025$, *** = $P < 0.001$.
^b Common names: PRF = Puerto Rican Flycatcher, RIT = Red-legged Thrush, Mb = Northern Mockingbird, BwV = Black-whiskered Vireo, YW = Yellow Warbler, YsBb = Yellow-shouldered Blackbird, GAG = Greater Antillean Grackle, BcO = Black-cowled Oriole, Tr = Troupial, BM = Bronze Mannikini.

TABLE 4. Fate of nests where Shiny Cowbird laid one or more eggs before host lays its eggs, Roosevelt Roads Naval Station ("RR") and Boquerón Forest ("BF") study areas, Puerto Rico, 1975–1981.

Species ^a	Locality	n	Number eggs laid by host after cowbird laid					Host mean clutch size	Host's activity		Cause of failure	
			0	1	2	3	4		Incubated	Raised offspring	Desertion	Predation
YW	RR	34	24	4	5	1	1.7	14	5	17	9	
YsBb	RR	25	20	4		1	1.4	8	5	20	1	
	BF	11	9	2			1.0	2	1	10		
GAG	RR	8	5			2	3.3	3	3	2		
BcO	RR	2	2							2		

^a YW = Yellow Warbler, YsBb = Yellow-shouldered Blackbird, GAG = Greater Antillean Grackle, BcO = Black-cowled Oriole.

(30% of nests failed owing to desertion) than at non-parasitized nests (10% deserted; χ^2 with Yate's correction = 29.5, $P < 0.0001$). Within a species, however, the desertion rates at parasitized and non-parasitized nests were not different, except for the Yellow Warbler population at Boquerón ($P < 0.05$).

Cowbirds occasionally deposited eggs in nests before the host had laid its first egg (Table 4). Typically, hosts abandoned these nests before laying their eggs, i.e., at nests where cowbirds laid first, 91% of all failures were due to desertion, with predation accounting for only 9% of the losses. Host desertion rates where parasites laid first were higher than those where the host had laid at least one egg. This was the case for Yellow Warblers ($\chi^2 = 4.4$; $P < 0.05$), Yellow-shouldered Blackbirds ($\chi^2 = 24.9$, $P < 0.001$), and Black-cowled Orioles ($\chi^2 = 8.6$, $P < 0.005$). Desertion rates of Greater Antillean Grackles remained about the same regardless of whether cowbird or host laid first.

Most hosts ($\bar{x} = 78\%$; four species) did not lay eggs in a nest where cowbirds laid the first egg. If the host did lay, however, its clutch size did not differ from that of other parasitized nests ($P > 0.05$, χ^2). Even when the hosts did not lay eggs, 20% of the pairs stayed with the nests to incubate all-cowbird egg clutches and 17% raised all-cowbird broods.

Probability of host desertion was inversely related to reproductive investment; i.e., number of host eggs deposited (Fig. 1). Hosts were less likely to desert nests containing completed clutches than nests where the host had not yet laid or where they had laid only one or two eggs: Yellow Warbler—D Max = 0.423 (Kolmogorov-Smirnov test; Null hypothesis: desertion rate for host with zero eggs = rate with one egg = rate with two eggs = . . . = rate with n eggs = 0; $P < 0.001$), Yellow-shouldered Blackbird—0.392 ($P < 0.0005$), Greater Antillean Grackle—0.441 ($P < 0.0002$). Rates of desertion for Yellow Warblers and grackles did not differ between parasitized and non-parasitized nests ($P > 0.05$, 2-way ANOVA; Fig. 1). Non-parasitized nests of Yellow-shoul-

dered Blackbirds had higher desertion rates than parasitized nests ($P < 0.02$, $F_{(2),1,2} = 169.9$), although the difference may have been an artifact of the small sample of non-parasitized nests ($n = 4$).

In summary, 42% of the resident non-raptorial land bird species were parasitized in my study areas. These species fell into two groups: those which were rarely or occasionally parasitized (2 to 17% of nests parasitized) and those that were regularly parasitized (>75% of the nests). Cowbird parasitism affected hosts by (1) depressing nest success an average of 41% below non-parasitized nests, and (2) reducing host productivity. Parasitized hosts produced 12% fewer eggs and fledged 67% fewer of their own chicks than non-parasitized pairs. Nevertheless, the total number of chicks (host + cowbird) fledged from parasitized nests was no different from the number fledged from non-parasitized nests; i.e., parasite chicks replaced some host chicks resulting in fewer host fledglings.

DISCUSSION

The first major finding of this study was that only some of the nesting species in the Puerto Rican mangrove community were regularly parasitized by Shiny Cowbirds. Those species were nevertheless parasitized at rates ranging from 75 to 100% of the nests examined. Second, I found that cowbird parasitism generally lowered host productivity.

No species were parasitized to an intermediate degree. Although parasitism rates described for most host populations range from low to moderate proportions of the nests (see Payne 1977 for examples), high rates have been reported for several populations: e.g., Red-eyed Vireo (*Vireo olivaceus*)—72% of nests parasitized (Southern 1958), Dickcissel (*Spiza americana*)—95% and Eastern Meadowlark (*Sturnella magna*)—70% (Elliott 1978), Rufous-collared Sparrow—66% (King 1973).

The high degree of exploitation I found in Puerto Rico is probably related to the Shiny Cowbird's recent arrival and expansion through

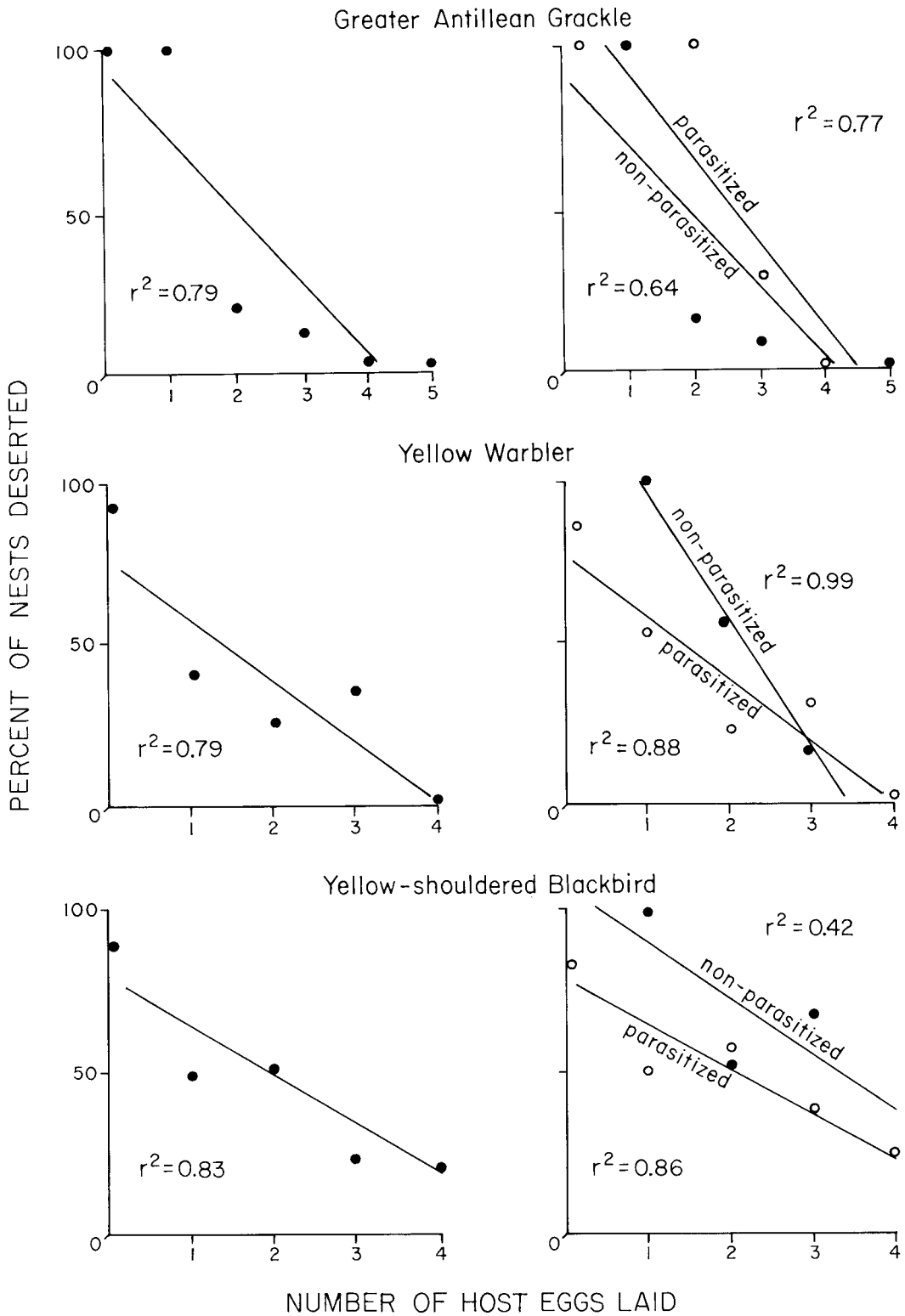


FIGURE 1. Association of nest desertion with owner's reproductive investment (i.e., number of eggs laid at the time of desertion) for Yellow-shouldered Blackbirds, Yellow Warblers, and Greater Antillean Grackles at Roosevelt Roads Naval Station study area, eastern Puerto Rico. For each species, the mean for parasitized and non-parasitized individuals is plotted in the left graph. In the right graph, parasitized individuals are plotted separately from non-parasitized birds. In the latter plots, circles represent parasitized individuals and dots depict non-parasitized birds.

an island whose resident birds presumably lack anti-parasite defenses; i.e., those species suitable as cowbird hosts and which lack effective anti-parasite defenses are heavily exploited. This pattern of heavy exploitation is not evolutionarily stable because the cowbird may eliminate certain host species or cause them to become rare through over-exploitation. A successful parasite should not eliminate its host. Logically, when hosts become so scarce that nests are limiting, it would be adaptive for the parasite to shift to another acceptable species. Concurrently, as nests of some species are more difficult to find because of their rarity, the rate of parasitism may also decline. However, this has apparently not yet occurred in the two Yellow-shouldered Blackbird populations I studied, despite their continued and accelerating decline (Post and Wiley 1976, 1977b; Wiley, unpubl. data). Shiny Cowbirds are extreme host generalists (Friedmann et al. 1977, pers. observ.). Even as they become rare, primary hosts (e.g., Yellow-shouldered Blackbird) may still be heavily parasitized. Cowbirds may sustain large populations by individuals shifting to other, less suitable hosts (e.g., Yellow Warblers, Greater Antillean Grackles). Meanwhile, the few remaining individuals of the primary host are still vulnerable to the cowbirds and continue to be parasitized whenever encountered. Although not well documented, local depression and extinction of host bird populations by a parasite may occur. After being parasitized by the Common Cuckoo (*Cuculus canorus*) with increasing frequency over the years, a population of Sedge Warblers (*Acrocephalus schoenobaenus*) became scarce and then disappeared (Owen 1933). Similarly, populations of Kirtland's Warbler (Mayfield 1960, 1965) declined precipitously after they encountered expanding populations of Brown-headed Cowbirds.

In Puerto Rico, overall nest success and productivity were lower at parasitized nests than at non-parasitized nests. Some parasitized species tended toward greater success than non-parasitized nests but these results are likely artifacts of small sample sizes.

Clutch size was usually smaller at parasitized nests versus non-parasitized nests. Two factors may have been working simultaneously to produce this effect: (1) if a cowbird lays an egg in a host's nest without simultaneously removing one of the owner's eggs, determinant layers may produce fewer eggs accordingly, and (2) Shiny Cowbirds commonly puncture and/or remove host eggs as they deposit their own eggs (Hoy and Ottow 1964; Post and Wiley 1977b; Wiley, unpubl. data). Some degree of error in estimating host clutch size is probable.

Punctured host eggs may have been removed by the cowbird or the host before I inspected the nest, so that they were never counted, leading to an underestimate of host clutch size. Thus, the first factor causes a real reduction of host egg production, whereas egg removal by cowbirds causes a smaller host clutch to be incubated but no reduction in number of eggs produced by the female. Subsequently, lower rates of hatching and fledging at parasitized nests are partly related to the initial reduced clutch size, but other contributing factors exist (see below).

Hatching rates at parasitized and non-parasitized nests differed considerably among host species. Fewer host eggs hatched at parasitized nests of some species than others, possibly because of two major factors: (1) differences in egg sizes cause uneven distribution of an incubating adult's heat, and (2) the sheer number of excess eggs from multiple parasitism may reduce the chance that the host's eggs will be adequately incubated (e.g., Black-cowled Oriole, Yellow-shouldered Blackbird). If the host's egg is smaller than the parasite's, it may not adequately touch the adult's body for proper incubation, and, consequently, fewer host eggs than cowbird eggs may hatch. Conversely, compared to hatching rates in the nests of other species, a lower proportion of cowbirds hatched in nests of grackles. I suggest that the smaller relative size of the cowbird egg resulted in poor contact with the foster parent's brood patch. Mayfield (1960) believed that the Brown-headed Cowbird eggs in Kirtland's Warbler nests have better contact with the incubating female than the warbler eggs, which are smaller.

Hosts can efficiently incubate only a certain amount of egg mass. The addition of cowbird eggs bolstered the clutches of several species above normal size so that the host may have been unable to cover all eggs, again resulting in lowered hatchability.

Fledging rates of host chicks were typically lower at parasitized nests than at non-parasitized nests, partly (as discussed above) because of reduced clutches at parasitized nests, but also because the foster adults could raise only a limited number of chicks. Perhaps brood size was limited by the adults' ability to care for a fixed maximum number of chicks; i.e., chicks hatching after the normal brood size was reached were eliminated through brood reduction.

Hudson (1920) and Gochfeld (1979) reported that the activities of Shiny Cowbird young may attract predators and thereby lead to excessive predation. In contrast, I found that most nests of Puerto Rican hosts were no

more likely to be depredated or abandoned than non-parasitized nests. Mayfield (1960) also reported no difference in predation rates between non-parasitized nests of Kirtland's Warblers and those that were parasitized by Brown-headed Cowbirds. However, I observed higher predation rates at parasitized Yellow-shouldered Blackbird nests than at non-parasitized nests. The reason blackbirds were exceptional is not clear, but may be related to differences between host and cowbird in their stealth at approaching the nest; i.e., cowbirds may be less surreptitious in their approach, allowing detection of the nest by avian predators. Rate of parasitism may be comparable with that for predation in that parasites use techniques and cues to locate host nests which are like those employed by some nest predators (Wiley 1982).

For the most part, desertion rates of parasitized species in my study populations were similar between parasitized and non-parasitized nests. That this defense is available in the behavioral repertoire of the host population and is regularly used in contexts other than avoiding parasitism suggests that desertion is a general response to nest disturbances. The higher frequency of nest desertion at parasitized over non-parasitized nests in one population (Yellow Warbler at Boquerón Forest) may indicate the adaptiveness of this defense behavior in avoiding parasitism. Hosts have had little time to evolve anti-parasite defenses, so that the single Yellow Warbler population with higher desertion rates among parasitized nests may represent an early manifestation of a pre-adaptive behavior application. This behavior may later become fixed if it is effective in reducing parasitism. Alternatively, gain of fitness in using desertion to avoid parasitism may not be great enough for it to become more common as a specific defense against parasitism.

In the parasitized species I studied, nest desertion may have been related to host reproductive investment; i.e., probability of desertion declined steadily with number of host eggs laid (see Clark and Robertson 1981 for similar results with hosts of the Brown-headed Cowbird). Early desertion of nests would result in minimal loss of time and energy investment. Also, the potential for successful renesting would be high with early desertion. However, pairs who deserted complete or nearly-complete clutches would encounter a delay of several days to construct a replacement nest (as would early deserters), build up energy reserves for an additional clutch, and lay the egg set. Although time limitations are not as constraining in Puerto Rico as they are in the north,

where breeding seasons are shorter, full recycling may preclude the production of one or more additional broods which are a regular part of the breeding cycle of many species in the tropics. Thus, there may be little reproductive gain, if any, by deserting a nest late in the laying sequence, whereas early desertion in response to disturbances is more likely to result in the production of additional clutches.

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RECENT PUBLICATIONS

The grouse of the world.—Paul A. Johnsgard. 1983. University of Nebraska Press, Lincoln. 413 p. \$42.50. The sixteen species of grouse and ptarmigans are distributed over desert scrub, grasslands, forests, and tundra of North America and Eurasia. As important game birds, they have received enormous attention yet no comprehensive treatment since Elliot's (1864-1865) monograph. That lack has now been admirably met with this book, the latest of Johnsgard's treatises on avian families. Its plan is conventional: a comparative overview of the group, followed by species accounts. The overview, however, is considerably fuller here than it was in his books on waterfowl, cranes, and shorebirds. Occupying nearly one-third of the text, it surveys grouse with regard to their evolution and taxonomy, physical and physiological traits, hybridization, breeding biology, population dynamics, social behavior and vocalizations, aviculture, hunting and conservation. The chapters on individual species are organized as to range and subspecies, measurements, identification, field marks, age and sex criteria, distribution, population density, habitat requirements, food and foraging, mobility and movements, reproductive behavior, and evolutionary relationships. The volume is generously illustrated with color and monochrome photographs, range maps, and the author's pen-and-ink drawings of displays. Obviously, this book will be widely useful as an inclusive source of information. In addition, it should remind North American researchers of how much is known about Old World grouse and ptarmigans, and facilitate more comparative evolutionary thinking about the group. Appendices, references, index.

Ecological study of bird hazards at Indian aerodromes. Phase II, First annual report (1982-83).—Salim Ali and Robert B. Grubb. 1984. Bombay Natural History Society. 96 p. Paper cover. No price given. Source: Bombay Nat. Hist. Soc., Hornbill House, Shahid Bhagat Singh Road, Bombay 400 023, India. Bird strikes to aircraft are a serious hazard in India because environmental conditions at airfields attract large numbers of vultures and kites, as well as other birds. Researchers of the Bombay Natural History Society have investigated this problem for several years, sponsored by the Aeronautics R&D Board in the Government of India's Ministry of Defense. This report opens with an analysis of Indian bird strike data and then examines the problem at three airports (additional to two which were studied earlier). Following chapters deal with potentially hazardous species of birds and with factors that attract them in and around airports. Follow-up work at the two first-studied airports and the causes of bird strikes enroute are discussed. In closing, the report makes several recommendations for preventive measures to reduce the numbers of problem birds at and around airports. Since these suggestions arise from an ecological study of the situation, they are sensible and likely to be more effective in the long run than the mass killing of vultures, which has been advocated as an immediate solution. These specific proposals have little or no application elsewhere, yet the approach leading toward them should be universal. Teachers of ornithology might well use this material as another example of the interactions between birds and human affairs—and how to alleviate them. Illustrations, appendices.