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IMPACT OF BROOD PARASITISM ON NEST SURVIVAL PARAMETERS AND SEASONAL FECUNDITY OF SIX SONGBIRD SPECIES IN SOUTHEASTERN OLD-FIELD HABITAT[1]

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Abstract. We monitored 259 nests of six Brown-headed Cowbird (*Molothrus ater*) hosts within old-field habitat on James Island, South Carolina during the 1997 and 1998 breeding seasons to determine the effect of parasitism on three nest-survival parameters (clutch size, hatching rate, and number of fledglings). We determined daily predation and parasitism rates, and probability of nest abandonment after parasitism to derive an estimate of seasonal fecundity. Clutch size of parasitized nests was reduced in four host species. Brood parasitism did not affect hatching rate in any species, and reduced the number of fledglings from only Blue Grosbeak (*Guiraca caerulea*) nests. Despite brood reduction during the nesting cycle, cowbird parasitism had little impact on seasonal fecundity of these host species because of low parasitism intensity, double-brooding behavior, and hosts' ability to raise their own young with cowbird young.

Key words: brood parasitism, Brown-headed Cowbird, Molothrus ater, *old-field habitat, nest parasitism, predation, seasonal fecundity.*

In North America, nest predation and Brown-headed Cowbird (*Molothrus ater*) parasitism are responsible for most songbird nest failures (Woodworth 1999). Brood parasitism and nest predation both act to reduce reproductive success in a given population. Nest predation usually results in the loss of an entire brood, whereas parasitism may result in partial reduction of nest contents, or no loss at all (Woodworth 1999). Hosts that accept cowbird eggs lose time and energy raising the cowbird young. The isolated or combined impacts of parasitism and predation on seasonal fecundity are determined by the species' propensity to renest after predation, abandon a parasitized nest, and/or initiate a second brood after a successful nesting attempt (Pease and Grzybowski 1995, Schmidt and Whelan 1999).

The majority of cowbird studies have taken place near the center of their historical range, where they have been in contact with hosts for thousands of years (Friedmann 1929, 1971, Clark and Robertson 1981, Branden et al. 1997). In the southeastern United States, however, where cowbirds occur in relatively low numbers, little is known of the impact of cowbird parasitism on host species (Lowther 1993). According to Breeding Bird Survey analyses, cowbirds are increasing in portions of southeastern North America more rapidly than in any other region within their breeding range (Sauer and Droege 1992). Here, we investigated the demographic consequences of cowbird parasitism for six species of songbirds in the southeast. Specifically, we determined daily predation and parasitism rates, and probability of nest abandonment after parasitism to derive an estimate of seasonal fecundity for these songbird species nesting within our study areas using Pease and Grzybowski's (1995) model of seasonal fecundity.

METHODS

STUDY AREAS

The study was conducted from March to September 1997 and 1998 in two old fields within the Dill Sanctuary of the Charleston Museum, James Island, Charleston County, South Carolina. These sites, approximately 2.1 km apart, were composed primarily of 4 to 8-year-old successional vegetation (1–6 m in height). Wax myrtle (*Myrica cerifera*), black cherry (*Prunus serotina*), sweetgum (*Liquidambar styraciflua*), sassafras (*Sassafras albidum*), black willow (*Salix nigra*), baccharis (*Baccharis halimifolia*), and privet (*Ligustrum vulgare*) dominated the shrub and tree vegetation. Ground cover and vines included goldenrod (*Solidago* spp.), broomsedge (*Andropogon virginicus*), ragweed (*Ambrosia artemisifolia.*), partridge pea (*Cassia fasciculata*), grapevine (*Vitis* spp.), trumpet vine (*Campsis radicans*), and blackberry (*Rubus* spp.). The study areas were surrounded by a strip of mixed pine and hardwood forest and bordered by the Stono River. We selected these study sites because they shared basic internal (successional stage, vegetation type and structure) and external landscape characteristics.

SAMPLING DESIGN AND FIELD METHODS

From April to August 1997 and 1998, we located nests within the study areas by watching adult birds for nest building and defense cues, and by systematic search-

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TABLE 1. Total number of nest days observed, clutch size, number of broods attempted during the season, first day in nesting cycle that the nest is susceptible to parasitism (t_e), last day that the nest is susceptible to parasitism (t_i), last day that the nest is susceptible to predation (t_f), day when a second brood is initiated after a successful nest (t_r), day when one half of the females are no longer in breeding condition (S_s), number of young fledged from a successful unparasitized nest (f_u), and number of young fledged from a successful parasitized nest (f_p).

Passerine Species	Total nest days	Clutch size	Broods	t_e	t_i	t_f	t_r	S_s	f_u	f_p
Blue Grosbeak	152	4	2	6	13	32	45	78	3.5	1.7
Indigo Bunting	136	3	2	5	11	30	43	91	3.0	1.0
Northern Cardinal	497	3	2	4	11	31	44	76	2.7	2.1
Painted Bunting	101	3	2	5	12	30	43	73	2.4	1.5
Red-winged Blackbird	331	3	2	5	12	31	44	76	2.5	2.0
Yellow-breasted Chat	187	3	1	5	12	29	42	52	2.9	2.3

ing. Each nest was checked every 2–4 days until the nest was successful or failed (Martin and Roper 1988). During nest checks, we noted adult activity around the nest, egg number, age of nestlings, or nest failure. We also noted all instances of parasitism and number of cowbird eggs in each parasitized nest.

We determined the cause of nest failure by examining nest structure, remaining nest contents, and contents below the nest. Nest failures were attributed to (1) parasitism—no host young fledged as a result of egg-removal by the adult cowbird and/or starvation of host nestlings, (2) abandonment due to parasitism—nest was abandoned when a cowbird egg was added, (3) abandonment due to predation—nest was abandoned after a predator removed one or more host eggs (not the entire clutch), (4) environment—nest was destroyed due to weather, vegetation growth, or poor nest construction, and (5) predation—entire clutch was removed/destroyed by a predator.

Predation type was identified as avian or reptilian (beak-puncture holes apparent in remaining nest contents and nest contents removed without disturbance) or mammalian (egg-shell pieces present, total nest destroyed or ripped from supporting vegetation (Best and Stauffer 1980). A nest was considered successful if ≥1 of the host species' offspring fledged.

STATISTICAL ANALYSES

Of the 16 species we found nesting in the study areas, we limited analyses for this study to 6. We used only species which were cowbird hosts and for which we had ≥100 nest-check days. We pooled data between years and study areas because host communities were the same and no differences in parasitism and predation rates were detected.

We used the Mann–Whitney U-test to determine the effect of parasitism on three nest-survival parameters: clutch size (mean number of eggs in nests monitored from onset of incubation), hatching rate (number of eggs hatched/total number of eggs in nest at hatching), and number of fledglings (mean number of young fledged from successful nests of host species). Significance was accepted at $P < 0.05$. Values presented are means ± SD.

We applied Pease and Grzybowski's model to our data, which uses several host breeding parameters as well as estimates of daily parasitism rate (p), daily predation rate (d), and the probability of abandonment after parasitism (a) to derive seasonal fecundity (Sf) for each species. Parameters used in the model included: (1) beginning of host susceptibility to parasitism (t_e), which we estimated as the day before host egg-laying began, (2) end of window of susceptibility to parasitism (t_i), which we estimated as nine days before host eggs hatched, (3) end of window to nest predation (t_f), which we estimated as the day that young fledged from the nest, (4) time in breeding season when the last nesting cycle was initiated relative to start date of nesting season (s_s), which we estimated as the initiation of the last nest within our sample, (5) mean number of host young fledged from unparasitized nests that were successful (f_u), and (6) mean number of host young fledged from parasitized nests that were successful (f_p) (Table 1). For a more complete description of the model, including equations and discussion, see Pease and Grzybowski (1995).

RESULTS

We monitored 259 nests of six Brown-headed Cowbird hosts within the two old fields during the 1997 and 1998 breeding season (March–August). Four of the species monitored were Neotropical migratory birds (Blue Grosbeak *Guiraca caerulea,* Indigo Bunting *Passerina cyanea,* Painted Bunting *Passerina ciris,* and Yellow-breasted Chat *Icteria virens*), and two were resident species (Northern Cardinal *Cardinalis cardinalis* and Red-winged Blackbird *Agelaius phoeniceus*).

Parasitism reduced nesting success during at least one stage of the nesting cycle for four host species (Table 2). Mean clutch size of parasitized nests of four host species was reduced and clutch-size reduction for Yellow-breasted Chats approached significance (Table 2). Hatching rate was not significantly reduced by parasitism (Table 2). Parasitism reduced the number of fledglings from successful Blue Grosbeak nests (Table 2). Avian and reptilian predation accounted for 84.1% of all nest failures. Parasitism directly caused 2.9% of nest failures through abandonment. Other nest failures were attributed to mammalian and fire ant (*Solenopsis* spp.) predation, environment, and abandonment due to partial predation.

TABLE 2. Total number of active nests monitored and mean ± SD (n − number of active nests during each nesting stage) for nest survival parameters of parasitized (P) and unparasitized nests (UP).

Species	Active nests		Mean clutch size		Hatching rate		Young fledged/successful nest	
	P	UP	P	UP	P	UP	P	UP
Blue Grosbeak	6	16	2.5 ± 1.1 (6)*[a]	3.5 ± 0.5 (11)	0.7 ± 0.2 (4)	0.9 ± 0.1 (10)	1.7 ± 1.0 (3)**	3.5 ± 0.5 (9)
Indigo Bunting	3	19	3.0 ± 0.0 (3)*	3.4 ± 0.5 (14)	0.5 ± 0.0 (2)	1.0 ± 0.1 (12)	—	3.0 ± 0.0 (8)
Northern Cardinal	5	87	1.7 ± 0.5 (4)*	2.9 ± 0.5 (78)	—	0.9 ± 0.2 (40)	—	2.7 ± 0.6 (33)
Painted Bunting	6	11	1.5 ± 0.7 (4)*	2.4 ± 1.2 (11)	0.7 ± 0.2 (4)	0.9 ± 0.3 (6)	1.5 ± 0.7 (2)	2.4 ± 1.2 (3)
Red-winged Blackbird	2	71	3.5 ± 0.7 (2)	3.1 ± 0.6 (67)	0.5 ± 0.0 (2)	0.7 ± 0.2 (27)	2.0 ± 0.7 (2)	2.5 ± 0.9 (16)
Yellow-breasted Chat	13	22	3.1 ± 0.9 (13)	3.5 ± 0.6 (19)	0.8 ± 0.2 (7)	0.8 ± 0.2 (9)	2.3 ± 1.2 (3)	2.9 ± 1.1 (8)

[a] Significant differences between parasitized and unparasitized nests; * $P < 0.05$, ** $P < 0.01$, Mann-Whitney U-test.

Parasitism rates of hosts ranged from <0.1–10% of available nests per day and nest predation rates ranged from 3.2–8.2% per day (Table 3). Seasonal fecundity for the six species ranged from 2.77–5.45 young fledged per female, and Yellow-breasted Chats, a single-brooded species, incurred the lowest fecundity (Table 3).

DISCUSSION

We used three nest survival parameters to isolate the impact of parasitism on six songbird species during the nesting cycle. These parameters had little impact on overall fecundity achieved by females across the breeding season, but they revealed whether and when brood reduction occurred during the duration of a host nest.

During the egg-laying period, cowbird parasitism reduced the mean clutch size of Blue Grosbeaks, Indigo Buntings, Painted Buntings, and Northern Cardinals. Cowbirds commonly remove at least one host egg before laying their own (Nolan 1978), and during this study, egg-removal behavior was observed directly at one Yellow-breasted Chat nest. Clutch-size reduction usually consisted of one host egg and resulted in partial nest failure.

The impact of parasitism on a nest during the incubation period was more difficult to assess. Most parasitized nests were depredated during the incubation period, leaving a limited sample with which to assess the impact of parasitism on hatching rate and fledging success. During the nestling period, no mortalities were linked directly to competition from the cowbird nestling or predators attracted by their begging; rather, any reduction in fledging success was most likely a result of clutch-size reduction during egg-laying and incubation.

The impact of parasitism on nest survival was ameliorated by low parasitism intensity (i.e., the mean number of cowbird eggs per parasitized nest). We seldom found more than one cowbird egg in a parasitized nest. Other studies have shown that approximately 40% of host nests are parasitized multiple times (Payne 1977, Lowther 1993). Low parasitism intensity is often correlated with reduced nest competition due to high host/cowbird ratio. Because of the reduced rate of multiply-parasitized nests, host nests are more likely to produce both cowbird and host young. Grzybowski and Pease (1999) predict that cowbird reproductive success may be greatest when the relative abundance of ejector hosts and cowbirds is low and few nests are abandoned after parasitism.

The isolated effects of parasitism on clutch size and number of fledglings did not directly affect female seasonal fecundity. As mentioned above, parasitism-induced brood reduction, detected during the egg-laying period, often did not significantly reduce the number of young fledged from a parasitized nest. Schmidt and Whelan (1999) note that when brood loss due to parasitism is low to moderate but nest predation is high, the effect of parasitism on seasonal fecundity may be undetectable. For all double-brooded species in this study, seasonal fecundity estimates appeared to be most closely correlated with nest predation. Because this study was conducted in a region of low cowbird

TABLE 3. Estimates (mean ± SD) of population parameters including: p – daily parasitism rate, d – daily nest predation rate, a – probability of abandonment after parasitism, and Sf – seasonal fecundity estimated using Pease and Grzybowski's (1995) model of seasonal fecundity.

Passerine Species	p	d	a	Sf
Blue Grosbeak	0.06 ± 0.05	0.03 ± 0.01	<0.001 ± 0.0004	5.45
Indigo Bunting	0.02 ± 0.05	0.03 ± 0.01	<0.001 ± 0.14	5.42
Northern Cardinal	0.02 ± 0.02	0.06 ± 0.01	0.66 ± 0.13	4.92
Painted Bunting	0.10 ± 0.01	0.06 ± 0.02	1.0 ± 0.25	4.13
Red-winged Blackbird	<0.001 ± 0.05	0.082 ± 0.01	0.53 ± 0.22	4.51
Yellow-breasted Chat	0.034 ± 0.01	0.062 ± 0.01	<0.001 ± 0.17	2.77

abundance with low to moderate parasitism, accurate estimates of daily parasitism and probability of abandonment could not be calculated. However, narrow estimates for daily nest predation rates showed that predation was high for most species. Although not applied here, this model could be used to predict at what point brood parasitism will begin to affect seasonal fecundity of hosts in areas of low cowbird abundance (Schmidt and Whelan 1999).

Double-brooding behavior in five of the six species was a major factor in minimizing the effect of predation on seasonal fecundity. The breeding-season length of Yellow-breasted Chats at our study site was not sufficient to allow two successful broods to be raised. Chats' seasonal fecundity was more than 2.0 (young fledged per female) lower than the average fecundity of the remaining five hosts, all double-brooded species (Table 3). Thus, a species' propensity to initiate a second brood after a successful nesting attempt is an important, perhaps the most influential, factor in determining breeding success (Pease and Grzybowski 1995, Schmidt and Whelan 1999).

Estimates for seasonal fecundity ranged from 4.1 to 5.5 for all double-brooded species. Various factors together may influence the success of these double-brooded species. Indigo Buntings, which displayed high seasonal fecundity, had the longest breeding season, and their daily parasitism and predation rates were among the lowest of the hosts. Blue Grosbeaks also achieved high seasonal fecundity despite experiencing high daily parasitism rates and brood reduction (average reduction = 1.8 young); however, parasitism-induced reduction of Blue Grosbeaks' fecundity was compensated for by its four-egg clutch and a relatively low daily predation rate.

Although most host populations were subject to brood reduction due to cowbird parasitism, this did not significantly reduce the number of host young fledged from most parasitized nests. Overall, parasitism had little impact on seasonal fecundity of host species in this study because of low parasitism intensity, double-brooding behavior in five of the host species, and these hosts' ability to raise the cowbird young with their own young. Daily predation rate and the species' propensity to renest after a successful nesting attempt were the most influential factors in determining seasonal fecundity of host species in this region of low cowbird abundance.

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ROOST SITE SELECTION OF GREAT HORNED OWLS IN RELATION TO BLACK FLY ACTIVITY: AN ANTI-PARASITE BEHAVIOR?[1]

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Abstract. We document a shift in roosting behavior of Great Horned Owls (*Bubo virginianus*) from winter and late spring to summer. During summer, Great Horned Owls roosted near the ground or exposed on open ground, whereas they chose concealed perches at mid-canopy level for the rest of the year as typical for forest owls. This shift of roosting behavior coincided with the emergence of ornithophilic black flies, which transmit avian malaria (*Leucocytozoon* spp.). The shift in roosting behavior was consistent with measurements of parasite exposure at different habitat positions. Black fly activity was highest at mid-canopy level, and almost no black flies were active on open ground. Ground-roosting was not caused by poorly developed flying capability of juveniles, because solitarily-roosting adult owls showed the same behavioral shift in a second year of study. Black flies and avian malaria are widely distributed, and the effect of the vertical distribution of these parasites in forests on roosting, nesting, and foraging of sylvatic birds deserves further study.

Key words: black flies, Bubo virginianus, *forest owls, Great Horned Owls,* Leucocytozoon, *parasitism, roosting behavior.*

Ornithophilic species of black flies (Simuliidae) can reduce the fitness of a host in a variety of ways (Møller 1990, Bennett et al. 1993). For example, black flies are a vector of *Leucocytozoon,* a protozoon causing avian malaria (Desser and Bennett 1993). As an example of possible consequences of disease, higher loads of *Leucocytozoon ziemanni* were associated with lower clutch sizes in female Tengmalm's Owls *Aegolius funereus* (Korpimäki et al. 1993). Detrimental effects may be directly caused by anemia. Blood extraction by the ectoparasite alone (or in concert with the blood parasite) may significantly contribute to anemia (Fitch et al. 1946, Richner et al. 1993, Hunter et al. 1997). In addition, there may be a cost of increased investment in immunological defense (Toft 1991, Richner et al. 1995).

We studied the response of Great Horned Owls (*Bubo virginianus*) to the 10-year population cycle of snowshoe hares *Lepus americanus* in the boreal forest from 1989–1992 (Krebs et al. 1995, Rohner 1996). Great Horned Owls are large and long-lived predators feeding mainly on lagomorphs, they defend long-term territories, and are widely distributed in North and South America (Voous 1988, Donazar et al. 1989, Rohner 1995, 1997). Several demographic parameters in Great Horned Owls were strongly affected by the population cycle of snowshoe hares (Rohner 1996).

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