

RESPONSES OF ZEBRA FINCHES (*TAENIOPYGIA GUTTATA*) TO EXPERIMENTAL INTRASPECIFIC BROOD PARASITISM

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ABSTRACT.—We experimentally examined the responses of captive Zebra Finches (*Taeniopygia guttata*) to intraspecific brood parasitism by adding two eggs to clutches at the onset (early treatment), in the middle (midtreatment), or at the end (late treatment) of egg laying. A comparison group was derived from nonparasitized nesting attempts of the same pairs. Experimentally parasitized nests were abandoned before hatching could have occurred at a much higher rate than were unmanipulated nests; most of the abandonment occurred in early-treatment nests. Females in the early treatment also appeared to curtail egg laying. A smaller proportion of eggs in experimentally parasitized nests survived, but survival of host and parasite hatchlings in such nests was equivalent. Within nests containing both host and parasite young, host young were heavier at day 10 posthatching; the cause of mass differences was not ascertained. Egg loss occurred relatively more frequently in manipulated than in unmanipulated nests, suggesting that clutch enlargement taxes parental capabilities. Received 14 December 1993, accepted 2 July 1994.

INTRASPECIFIC BROOD PARASITISM may be an important selective agent in birds as a result of their oviparous habits and the high degree of parental care displayed by many species. By laying eggs in the nests of conspecifics, brood parasites potentially are able to avoid costs and/or constraints that limit the evolution of interspecific parasitism (Hamilton and Orians 1965, Payne 1977). Potential limitations on interspecific parasitism include heterospecific recognition of eggs and young by hosts, poor fit between developmental progression and offspring needs of host and parasite young, and sexual imprinting of parasite young on the host species. Thus, while interspecific brood parasitism has evolved infrequently, intraspecific parasitism has arisen repeatedly (Yom-Tov 1980) and may be maintained in populations via frequently-dependent mechanisms. It is likely that selection has also strongly favored the evolution of defenses against intraspecific brood parasitism (Rohwer and Freeman 1989).

Despite the potential evolutionary importance of intraspecific brood parasitism and the

growing recognition of its widespread occurrence (Yom-Tov 1980, Gowaty and Karlin 1984, Brown and Brown 1989, MacWhirter 1989, Rohwer and Freeman 1989), there has been relatively little experimental attention paid to the phenomenon (but see Lanier 1982, Briskie and Sealy 1987, Kendra et al. 1988). Accordingly, we decided to study behavioral defenses against brood parasitism in a laboratory colony of Zebra Finches (*Taeniopygia guttata*).

Zebra Finches are a good species in which to study defenses against intraspecific brood parasitism because recent evidence indicates that it occurs in both free-living (Birkhead et al. 1990) and captive (Burley et al. in press) populations. Also, Zebra Finches show several life-history traits that may favor intraspecific brood parasitism as a secondary reproductive tactic. These include: high rates of nest predation (Burley and Zann unpubl. data), which may favor placing eggs in more than one nest; aggregated nesting that may result from nest-site limitation as well as lack of territoriality (Goodwin 1982); irregular or prolonged breeding intervals that permit multiple clutch attempts per female (Immelmann 1962); and ecological circumstances that favor attempted reproduction by young and inexperienced females (Hamilton and Orians 1965, Rohwer and Freeman 1989).

Defenses against intraspecific brood parasitism can be dichotomized into prelaying and

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postlaying tactics. Prelaying defenses include nest guarding, nest crypsis, and nesting asynchrony (Yom-Tov 1980, Møller 1987). Possible postlaying defenses include abandonment of the nest (Yom-Tov 1980), egg eviction (Bertram 1979, Møller 1987, Brown and Brown 1989), selective egg burial (Clark and Robertson 1981), and discrimination against parasitic offspring. We experimentally investigated postlaying defenses by adding eggs to clutches at various times in the laying sequence and following the fates of manipulated and unmanipulated clutches.

METHODS

Zebra Finches are socially monogamous estrildines with strong pair bonds. They display extensive biparental care of their altricial young. Clutch size varies from three to eight eggs (Goodwin 1982); mean clutch size ranges between 4.5 and 5 eggs in both captive and free-living populations (Burley unpubl. data). Clutches begin to hatch 12 to 14 days after the first egg is laid; incubation typically begins with the third egg. Young remain in the nest about 18 days in the laboratory and somewhat longer under field conditions. Fledglings are cared for by their parents for an additional 10 to 14 days.

Housing and experimental design.—Thirty young, never-mated adults of each sex were released into a free-flight aviary (54 m³) in the Shelford Vivarium of the University of Illinois. All founders had wild-type plumage. Resources provided *ad libitum* included commercial finch mix, water, grit, cuttlebone, and hatching food. Vitamins, eggs, vegetables, and fruits were provided regularly. Straw and cotton batting were provided liberally for nesting material. The aviary contained two plastic nest cups for each pair. Photoperiod was constant (14 L:10 D).

Throughout the study (March–October 1990), nests were checked daily between 1000 and 1400 CST, and the presence of eggs, hatchlings, and fledglings was recorded. We also recorded egg condition: warm or cold; buried or not; cracked, missing, or discolored. Eggs were marked on the day laid with small (2-mm), numbered plastic markers manufactured for marking bees. A single number was applied to the air end of each egg with water-soluble glue. A preliminary trial had established that these markers do not affect parental acceptance, hatchability or juvenile mortality rates. Hatchlings were marked on their posterior down feathers with any of several colors of nontoxic marking pen (Burley 1986). When nestlings reached 8 g, they were banded with numbered metal bands. Nestlings were weighed at 10 days of age. Young were removed from the aviary at 40 to 50 days of age. We ascertained social parentage by direct observation of parental activities of color-banded adults (Burley 1985) from an adjacent, darkened room.

The experimental manipulation involved adding two eggs to selected clutches. We have observed as many as three brood parasitic eggs per clutch in the laboratory, but one is probably the most common number. We decided to use two eggs per clutch in the manipulation for several reasons, the most important being that we were concerned that our manipulation did not provide appropriate behavioral cues to parasitization. We believed that birds would be more likely to discern a two-egg manipulation in the absence of other appropriate cues.

We obtained "parasite" eggs from breeding pairs in an adjacent aviary that was maintained under similar conditions. Parasite eggs were always less than 48 h old (usually less than 24 h old) and were unincubated. In most cases, both parasite eggs added to a particular host clutch came from the same donor clutch.

In the experimental aviary, selected nests were assigned to one of three treatments. Two "parasite" eggs were added to all "host" nests in these treatments, but the timing of this manipulation varied. In the "early treatment," the first parasite egg was added when we anticipated that a particular host female was about to begin a clutch. The second egg was added on the day the first host egg appeared. In the "mid-treatment," we added the first parasite egg on the day the second host egg was laid, and the second parasite egg on the day the fourth host egg was laid. In the "late treatment," the first parasite egg was added on the day the fourth host egg was laid, and the second parasite egg was added the day after the last host egg appeared.

Availability of fresh parasite eggs was a primary consideration in determining whether a particular nest was assigned to an experimental treatment. Nests selected for manipulation were assigned to treatment using a sequential design to minimize any temporal pattern among treatment groups. To locate early-treatment host nests, we observed nests closely during the early nest-building phase. When we determined that a pair had been nest building at the same site for two days, we added a donor egg. In five early-treatment trials, pairs abandoned after the first parasite egg was added to their nest, but before the first host egg was laid. These trials are excluded in all data analyses, resulting in a conservative estimate of abandonment in parasitized clutches.

Following manipulation, observations were made on experimental nests to determine whether parents abandoned. A nest was considered abandoned if the eggs were found to be consistently cold or buried before the young could have hatched (12 days after first host egg laid). Most abandonment occurred before or shortly after incubation commenced. Typically, parents were observed reneesting nearby following abandonment. Clutches that became cold after they were scheduled to hatch were classified as "failed to hatch" rather than as abandoned; all such clutches

remained warm for at least 15 days after the first host egg had been laid.

When eggs in manipulated nests were scheduled to begin hatching, nests were observed closely to ascertain the identity of the hatching inside each marked egg. In a few cases, parasite and host young hatched synchronously and could not be discriminated.

Unmanipulated nests were treated similarly to manipulated nests. Nests were inspected daily in both groups. All eggs received "bee" numbers and were handled regularly; hatchlings were marked and banded using identical procedures. Unmanipulated nests were used for statistical comparisons as described below.

Statistical procedures.—In a few cases, a pair was inadvertently assigned twice to the same treatment. When this occurred, the first manipulated nesting attempt of a given pair was used for analyses involving dichotomous data (e.g. nest abandonment), and mean values were used for other attributes (e.g. clutch size). The same procedure was employed for control nests. Distribution-free statistical tests were employed for all analyses (Zar 1974). The Fisher exact test was used to examine the relative frequency of abandonment across experimental treatments and relative survival of host and parasite eggs and young. The Wilcoxon matched-pairs signed-rank test was used to make comparisons between manipulated and unmanipulated nests. The unit of analysis here is the pair; mean values are based on all available data for experimental and control nests of each pair for which data are available. Where appropriate, Bonferroni adjustments in *P*-values have been made for multiple comparisons (Rice 1989). All tests are two-tailed.

RESULTS

Abandonment.—Excluding nests deserted before hosts began laying (see Methods), 30 nesting attempts of 22 pairs were manipulated. Of these, 11 pairs abandoned one or more nests; abandonment rates varied between 33 and 100% for all pairs. Fourteen of the 22 pairs also had nonmanipulated clutch attempts during the experimental interval. Two pairs abandoned some fraction (16 to 33%) of their unmanipulated clutch attempts. The tendency of pairs to abandon manipulated nests more frequently is statistically significant ($n = 11$, with ties excluded; $T = 3.5$, $P < 0.01$; in all cases, tied values reflect pairs with no abandonment in either group). Within the manipulated nests, abandonment also varied among treatments, with the highest incidence occurring in the early treatment (Table 1; Fisher 2×3 exact test, $P = 0.006$).

In most cases, abandonment was preceded by burial of the freshly laid clutch. Five of 11 pairs

TABLE 1. Clutch abandonment among manipulated nests. Fisher exact test, $P = 0.006$.

Treatment	Number of nests	
	Abandoned	Not abandoned
Early treatment	7	2
Midtreatment	3	7
Late treatment	2	7

began burying the clutch and/or initiated nest searching within a day of the appearance of the first parasite egg. In such cases, egg laying was curtailed. This response occurred in all three treatments. In all but one case of abandonment, the clutch was completely buried within 48 h after the second host egg was laid. Pairs re-nested either in the same location or at a nearby site. Clutches that were abandoned are not included in measurements of clutch attributes (e.g. clutch size).

Incubation interval.—The interval between the onset of host egg laying and hatching of the last egg might have been lengthened by the experimental addition of two eggs, either as a result of the late-treatment manipulation (which could result in delayed hatching of the last egg), or from increased costs of incubation of enlarged clutches (Coleman and Whittale 1988). We found no evidence of such a trend (median egg interval, excluding first parasite eggs of early treatments, for both manipulated and unmanipulated nests was 18 days; $n = 13$, $T = 38.5$, $P > 0.5$).

Fates of young.—We compared the tendencies of parasite and host young to hatch and fledge. Young of unknown origin were excluded from analysis. There is no indication of differential hatchability or survival of host versus parasite young (Table 2). Of the nine surviving parasite young, two were reared in early-treatment nests, four in midtreatment nests, and three in late-treatment nests.

Clutch and brood size.—Manipulated clutches were significantly larger at clutch completion than unmanipulated ones by exactly the number of eggs (2) added during the manipulation. To further ascertain that laid clutch size of non-abandoned host clutches was unaffected by the experimental manipulation, we compared clutch sizes of nonabandoned early-treatment and midtreatment nests with those laid by the same pairs in unmanipulated nests; laid clutch sizes

TABLE 2. Fates of eggs and young hatched in non-abandoned host nests. Fisher 2×2 exact tests performed on number of host and parasite young surviving versus not surviving for each developmental interval (egg stage to hatching, hatching to fledging, and fledging to independence). With Bonferroni adjustments for multiple comparisons, all $P > 0.50$.

Number	Egg type	
	Host	Parasite
Eggs	70	30
Hatchlings	43	16
Fledglings	35	10
Achieving independence	28	9

did not differ between these groups (median = 5 for both groups; $n = 8$, $T = 3$, $P = 0.20$).

Despite the larger total clutch size of the manipulated nests, neither number of hatchlings nor final brood size (number of fledglings produced) varied between manipulated and unmanipulated nests (Table 3). Manipulated clutches, however, sustained significantly more loss during the egg phase (Table 3).

Causes of egg loss included failure to hatch (egg remaining in nest well after scheduled hatching time), and burial, breakage, or disappearance of eggs during incubation. Absolute incidence of egg loss from all sources was greater for manipulated clutches. Reasoning that loss through burial, breakage or disappearance of eggs was more likely the result of behavioral decisions made by parents than was loss through hatching failure, we compared the relative incidence of hatching failure (percent of all egg

TABLE 3. Clutch size, offspring survival, and reproductive loss for manipulated and unmanipulated clutches.

	Manipulated ^a	Unmanipulated ^a	P^b
Reproductive component			
No. eggs	7	5	0.01*
No. hatchlings	4	3.2	0.48
No. fledglings	2	3	0.97
Reproductive loss			
Egg loss	2.5	1.5	0.01*
Hatchling loss	0	0	0.39
Fledgling loss	0	1	0.33

^a Group medians derived from mean values for each of 14 pairs.

^b Wilcoxon matched-pairs signed-rank test, normal approximation (Wilkinson 1990). Bonferroni adjustment for multiple comparisons (*, $P < 0.05$).

loss occurring through hatching failure) for manipulated and unmanipulated clutches. In manipulated nests, median hatching failure for the 14 pairs accounted for 50% of all egg loss; for unmanipulated nests, hatching failure accounted for 10% of egg loss ($T = 13.5$, $n = 12$ [ties excluded], $P = 0.06$).

Mass of young.—We compared masses at day 10 of parasite and host young in nests in which individuals belonging to both categories survived. Analysis was based on the mean mass of young of each category within nests. Masses of host young (median = 8.42 g) were greater than those of parasite young (median = 7.44 g; $n = 7$, Wilcoxon $T = 2$, $P = 0.05$).

DISCUSSION

Abandonment.—Zebra Finches clearly responded to experimentally induced intraspecific brood reduction that occurred early in the laying sequence by abandoning the affected clutch attempt and beginning anew. Later in the laying sequence, this response waned (Table 1). The decline in abandonment could have resulted from lowered ability of birds to recognize parasitism initiated late in the laying sequence, although the rapid response by parents that abandoned in all three treatments suggests that detection of parasitism may not be a constraint.

An alternative possibility is that the cost-benefit ratio of abandoning changes over time, such that the profitability of abandoning declines (Droge and Burley unpubl. manuscript). As incubation progresses the interval of time needed to complete the current clutch decreases, while the time needed to complete a new clutch, following abandonment of the current one, remains constant. Thus, the benefit of abandoning declines if time to clutch completion is an important ecological constraint, as is likely to be the case (Immelmann 1962). Also, Zebra Finches experience high rates of nest predation in nature during the egg phase (Burley and Zann unpubl. data); thus, the value of a clutch increases if it has escaped predation for a significant interval.

Support for the possibility that differences in the benefit-cost ratio influence the decision to abandon is provided by the observation that females of early-treatment nests that were abandoned appeared to curtail the egg-laying process. Most females at abandoned early-treat-

ment nests laid no more than a single egg following the initial act of parasitism. Following abandonment, they again laid a full clutch at the same or at a different nest. The aviary was searched regularly for the "leftover" eggs of the abandoned clutches, but the eggs were not found. Moreover, pairs often frequently adopted prelaying behaviors almost immediately following abandonment. By curtailing the egg-laying process and recycling to lay full clutches promptly, females minimized both time and energy costs resulting from abandonment.

Discrimination of host versus parasite young.—Parasitism did not result in differential rejection of eggs or parasite young, suggesting that parents cannot differentiate their own eggs/young from the parasite young. Our results indicate that Zebra Finches, like some other passerines (Lanier 1982; but see Rothstein 1982), lack the capacity for selective egg burial. This is not surprising since Zebra Finches lay plain white eggs. Within experimental clutches, masses of parasites were somewhat less than those of host young, suggesting possible parental discrimination of young (e.g. Robertson 1991). If parental-discrimination abilities were very good, a more pronounced rejection of parasite young would be more adaptive than a quantitative response. If parentage is a probabilistic estimate, however, a graded response to parental investment is more plausible. One alternative explanation for the lower mass of parasite young is that they grew more slowly because of late hatching. This possibility can be cautiously rejected: these young did not hatch off schedule for the clutch, and their hatch order distribution was very similar to that of the surviving host young. Typically, hatching of a clutch of Zebra Finches takes place over several days and, for surviving young, there is no clear relationship between hatch order and mass at day 10 (Burley unpubl. data). Moreover, any such relationship would be largely offset here by the use of mean values of day-10 mass within the brood as the basis of comparison (see Results). Possible alternative explanations for the lower mass of parasite young include that parents are for some reason (e.g. genetic complementarity) better able to care for their own offspring or that nestling interactions (e.g. Trivers 1974) result in lower masses of parasite young.

Significance of hatch failure.—The high incidence of hatching failure in manipulated clutches suggests that enlarged clutch size im-

poses some cost to Zebra Finches. Possible costs include: (1) inability to provide adequate cover for enlarged clutches (e.g. Delnicki et al. 1976); (2) increased physiological cost of incubation (Coleman and Whittale 1988); and (3) insufficient parental attention to egg caregiving (e.g. rotating positions of eggs). The first and third costs seem more likely to lead to partial hatching failure of clutches than the second, for which the costs should be either deferred past hatching or born equally among all eggs. Coleman and Whittale (1988), for example, found for the Bengalese Finch (*Lonchura striata*) that increased clutch size resulted in hatching delay of the entire clutch and increased food consumption during incubation by parents. We did not find a hatching delay in our study. The adequate-cover hypothesis may be applicable to some taxa, such as ducks (Anatidae), in which clutch size is sometimes increased substantially by parasitism (Andersson and Eriksson 1982 and references therein), but in our study all experimentally altered clutches were within the naturally occurring range. Perhaps parental attentiveness to eggs does not increase to the extent needed to maximize hatching success of enlarged clutches. Occasional parental inattentiveness to eggs could lead to sporadic chilling or other damage to eggs that causes increased rates of hatching failure without causing total hatching failure. It is clear that high hatching failure is not an adaptive response to parasitism per se, since host eggs were affected at the same rate as parasite eggs.

Cues to parasitism.—One limitation of our experimental design is that we could not provide appropriate cues of parasitization, such as interest shown in a nest by a would-be brood-parasitic female. The seeming failure of finches to respond to mid- and late-treatment manipulations may have resulted in part from an absence of appropriate behavioral cues. During the course of this experiment, for example, a case of brood parasitism occurred naturally that corresponded reasonably well to a late-treatment manipulation. As determined by distinctive egg shape and laying sequence of marked eggs, a female added three eggs to another's clutch of five, commencing on the day the last host egg was laid. All three of these eggs disappeared at hatching or shortly thereafter, while all hatching host young were cared for. (Brood reduction typically involves selective parental removal of live young from the nest [Burley

1986].) Egg-shape differences in this case were highly distinctive and might conceivably have provided a cue in addition to late hatching (all host eggs hatched before parasite eggs) and the behavior of the brood-parasitic female.

Because of the lack of natural cues to parasitic events, we do not feel it meaningful to evaluate the relative profitability, from a parasite's perspective, of early versus late parasitism in this experiment. While the high frequency of abandonment in the early treatment suggests that intraspecific nest parasites should avoid this period for parasitism, opportunities for parasitism may be greatest at this time, since incubation has not commenced. Moreover, "hosts" are occupied with courtship and mate-guarding activities early in the nesting cycle, which may decrease their attentiveness to behavioral cues of parasitism.

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