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AN EXPERIMENTAL TEST OF THE HAMILTON-ORIANS HYPOTHESIS FOR THE ORIGIN OF AVIAN BROOD PARASITISM[1]

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Abstract. Hamilton and Orians (1965) hypothesized that obligate interspecific brood parasitism might evolve when nest destruction during laying leads birds to lay subsequent eggs in their clutches in conspecific nests. It is unknown whether facultative parasitism after nest destruction is common in birds, but it is a reasonable expectation since many nesting species, especially colonial ones, commonly practice intraspecific parasitism. Red-winged Blackbird (*Agelaius phoeniceus*) nests were removed after females laid their first eggs and other nests in the same colonies were monitored to determine whether the affected females laid subsequent eggs parasitically. No parasitic eggs appeared in other nests and, in some cases, fresh eggs were found the next day at the sites of the removed nests. Thus the initial response in the Hamilton-Orians hypothesis is uncommon or absent in Red-winged Blackbirds. A literature review and new data indicate that Red-winged Blackbirds lack defenses likely to forestall brood parasitism so the failure to elicit parasitism experimentally and its rarity or absence in nonmanipulative studies of this species is enigmatic

Key words: Agelaius phoeniceus; *interspecific brood parasitism; intraspecific brood parasitism; nest loss; Red-winged Blackbird.*

INTRODUCTION

While studies of the coevolution between parasitic birds and their hosts have greatly increased our understanding of this interaction (Davies et al. 1989, Rothstein 1990), little is known about the evolutionary origin of brood parasitism. Many early investigators viewed obligate interspecific parasitism as something of a last ditch strategy that a population adopted when normal nesting behavior degenerated and became inefficient (Herrick 1910, Hohn 1962, Weller 1959, Friedmann 1960). Hamilton and Orians (1965) first pointed out that this class of "degenerative hypotheses" invokes a most unlikely evolutionary mechanism, namely a progressive loss of efficient, finely tuned adaptations by an entire population or species. These authors also proposed a mechanism for the origin of brood parasitism that is in agreement with modern evolutionary theory. They suggested that a nonparasitic bird whose nest was destroyed during egg laying would have to lay subsequent eggs somewhere and that another bird's nest could provide the suitable stimuli for laying. They further suggested that such a scenario is most likely in colonial species as this would provide a female with nearby nests identical to her own. After becoming established, such intraspecific parasitism by females making the best-of-a-bad-situation could lead to parasitism of other species. More recent work since Hamilton and Orian's paper has shown that intraspecific parasitism is a regular feature of the breeding biology of many bird species (Yom-Tov 1980, MacWhirter 1989, Lyon and Eadie 1991, Petrie and Møller 1991) and that it is due in some cases to nest destruction during laying (Yom-Tov 1980, Emlen and Wrege 1986, Feare 1991). Thus, nest destruction and consequent laying in a conspecific's nest is a reasonable expectation for many species and the Hamilton-Orians hypothesis can therefore apply to both intra- and interspecific parasitism.

Here, I present an experimental test of the Hamilton-Orians hypothesis. I determined whether laying Red-winged Blackbirds (*Agelaius phoeniceus*) deposited eggs in conspecific nests after I removed their own nests. While comparable experiments have been done on two species that have high rates of intraspecific parasitism (Emlen and Wrege 1986, Feare 1991, Stouffer and Power 1991), there have been no experimental attempts to determine whether nest loss can trigger parasitism in species that are known not to have a high level of intraspecific parasitism. Two recent studies (Gibbs et al. 1990, Harms et al. 1991) found little or no intraspecific parasitism in this blackbird. Thus if nest destruction during laying elicits parasitism in this species, the scenario hypothesized by Hamilton and Or-

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ians may be a potential stepping stone towards parasitism for all or most bird species. However, because few bird species have become obligate interspecific parasites, one would have to hypothesize that additional features facilitate the change from intraspecific parasitism to parasitism of other species.

The Red-winged Blackbird is a good choice for this sort of experiment. First, it is a colonial breeder and recent reviews have shown intraspecific parasitism to be common among such species (MacWhirter 1989, Rohwer and Freeman 1989). Secondly, nest failure during laying is common in Red-winged Blackbirds (19% of 6,787 nests, Harms et al. 1991) so the first event in the Hamilton-Orians scenario does indeed occur. Most failures involve predation that leaves nests intact but empty (pers. observ.). However, nests of this marsh-nesting species are sometimes literally destroyed when rising water after rain storms completely covers those built close to the usual water level (pers. observ.). Lastly, the Red-winged Blackbird is in the same subfamily (Icterinae) as one of the six clades of obligate interspecific parasites, the cowbirds (*Molothrus* spp.), and may therefore possess features that predispose it towards the evolution of brood parasitism.

My manipulations failed to elicit parasitism in Red-winged Blackbirds. Since it has been suggested that defenses against parasitism may forestall the evolution of intraspecific parasitism (Rohwer and Freeman 1989), I also discuss previous work assessing possible host defenses in these blackbirds and present new data on experiments designed to test for a defense against parasitism. Specifically, I show how Red-winged Blackbirds respond to conspecific and nonmimetic eggs placed in their nests before they commence laying. Such eggs are usually removed in species that experience high rates of intraspecific parasitism (Emlen and Wrege 1986, Stouffer et al. 1987, Brown and Brown 1989).

METHODS

I removed nests after females laid their first egg. This assured that females were scheduled to lay more eggs as Red-winged Blackbird clutches nearly always have at least two eggs (Payne 1969) and average 3.3 eggs at my study sites near the campus of the University of California, Santa Barbara County, California ($n = 211$ nests studied in 1977; K. F. Kundert, pers. comm.). All nests that were visited on the first day of laying were removed unless there was another such nest within 25 m. In these cases, I randomly chose one of the suitable nests for removal. Nest removals were done from 09:03 to 10:30 (three cases) or 16:17 to 17:00 (six cases) PST between 19 April and 7 May 1974. Red-winged Blackbirds almost always lay at 24 hr intervals and do so about 17 min after sunrise (Scott 1991), which means that nest removals occurred at least 3 hr after egg laying. In birds, ovulation of the next egg in a clutch occurs shortly after the previous egg has been laid. Thus, at the time of the removals, eggs had been traveling down the oviduct for at least 3 hr, a time period during which they would have received all or most of their full complements of albumen (Sturkie 1976). In Brown-headed Cowbirds (*Molothrus ater*), which lay about 25 min earlier than Red-winged Blackbirds (Sott 1991), eggs are half way down the oviduct by 08:00 and have soft shells by 12:00 (Payne 1965). It is highly unlikely that birds can resorb such eggs and thus I assume that all manipulated females were physiologically committed to laying an egg the next day. However, it is possible that females resorbed ova scheduled to be the third and later eggs in a clutch.

I removed nests in two colonies 1.7 km apart. These colonies were in "Gas Tank Marsh" and "Torres Towers Marsh" and each had respectively, 24 and 20 nests with the two most distant nests in each colony 36 and 94 m apart. Each colony provided at least four active nests with eggs during each nest removal but was small enough so that I could find all blackbird nests. My *a priori* criteria for identifying parasitic eggs were the appearance of two eggs in one 24 hr period during laying or the appearance of an egg three or more days after laying ceased (MacWhirter 1989). To differentiate between host and parasitic eggs, I numbered the eggs in all nests. All nests were visited daily and I searched the ground or water within 1–2 m around the site of each removed nest in case females laid their second egg at the original nest site.

One removed nest (number 2) was 24 m from the nearest blackbird nest. To provide this female with a nearby potential host nest, I attached a fresh Red-winged Blackbird nest to cattails 1.5 m and in full view from the original nest site at the time of nest removal. Some nests were inactive as they were never seen to have eggs or nestlings during the study but were fresh nests

TABLE 1. Nest removal results.

			Number of other nests[c]			
Removal number[a]	Date	Time[b]	Empty	With eggs	With nestlings	Results after one day
1	Apr. 19	PM	0 (3)	1 (4)	0 (2)	egg 65 cm from nest site
2	Apr. 19	PM	0 (3)	1 (4)	0 (2)	egg 37 cm from nest site
3	May 5	AM	3 (9)	4 (9)	0 (2)	no egg found
4	May 7	PM	3 (7)	2 (10)	1 (2)	no egg found
5	May 9	PM	4 (7)	3 (10)	0 (1)	no egg found
6	May 2	PM	1 (9)	1 (5)	0 (2)	egg 78 cm from nest site
7	May 4	AM	1 (7)	0 (4)	0 (5)	no egg found
8	May 5	AM	2 (6)	3 (4)	2 (4)	no egg found
9	May 7	AM	1 (6)	0 (4)	0 (6)	no egg found

[a] Nest removals 1–5 were done in Gas Tank Marsh while 6–9 were in Torres Tower Marsh.

[b] AM and PM mean that nests were removed between 09:03–10:30 and 16:17–10:00 PST, respectively.

[c] These are the number of other nests in each category (empty, with eggs or with nestlings) on the day of each nest removal. The first number in each entry is the number of nests within 5 m of each removed nest, while numbers in parentheses are the number of nests in the entire colony.

built during the current season. I placed single Red-winged Blackbird eggs or artificial Brown-headed Cowbird eggs (Rothstein 1975) in three of these six inactive nests to give the appearance that they were active and therefore suitable for parasitism. Red-winged Blackbirds show no discrimination between their own and cowbird eggs, which are nonmimetic (Rothstein 1975), and readily incubate clutches containing only the latter (Rothstein 1982).

To assess how these blackbirds respond to eggs that must be those of a parasite, I placed single artificial cowbird (Rothstein 1975) or real blackbird eggs in active and completed but empty blackbird nests in New Haven and Fairfield counties, Connecticut in 1969. Although done originally to test for responses to cowbird parasitism, these experiments are directly relevant here.

RESULTS

Table 1 presents the results of each nest removal and the numbers of potential host nests in each colony at the time of the removal. I never found an extra "parasitic" egg in any nest. On three occasions, I found intact fresh Red-winged Blackbird eggs within 1 m of nest sites on the day after removals. Two of these eggs were floating in water and were barely visible as fresh eggs float mostly below the surface. It is likely that some or all of the remaining six females also laid near their original nests but I was unable to find their eggs. I continued to search around each nest site on the second and third day after removals but found no further eggs. Removals done in the afternoon, as opposed to the morning, tended to result in an egg being found (3 of 5 versus 0 of 4, Table 1) but the trend was not significant ($P > 0.05$, Fisher exact test). The three removals that led to found eggs were the first three that were done and this temporal trend was significant ($P < 0.025$, Mann-Whitney U-test).

My methods would not have detected cases in which a manipulated female laid her second egg in a nest at which laying was occurring and also removed the host's latest (i.e., unnumbered) egg. However, only three removals were on days that other females were laying and two of these were cases in which I found fresh eggs at the removal sites. Thus, this confound could have affected only one nest removal but given the lack of parasitic laying by other females, it seems unlikely that this female would be such an efficient parasite as to remove a host egg. Such removal is absent to rare even in species with frequent intraspecific parasitism (Brown and Brown 1989). I would not have detected parasitism by a manipulated female if a nest in which she laid was destroyed before my next visit. A nest was depredated between visits and in the same colony in which I initiated a removal in only one case. But in this instance, there were three other nests closer to the removed one.

In the egg addition experiment, I placed a single artificial cowbird egg in each of 11 empty blackbird nests. Red-winged Blackbirds accepted the cowbird egg and laid normal clutches in seven of these nests. In three cases, the nest was deserted and no blackbird eggs were laid. The last nest was also deserted but the cowbird egg was removed from it. All four empty nests in which I placed a blackbird egg received normal clutches. Thus at none of these 15 nests did birds show what would have been the most efficient response to parasitism, i.e., ejection of the parasitic egg followed by laying in the same nest. In addition, the desertion rate of empty nests that received cowbird eggs was not significantly higher than that of other nests that did not receive an egg before laying began ($P > 0.1$, Fisher exact test on 4 of 11 versus 2 of 19). These unmanipulated nests were found before laying began and in the same year and area as the experimental nests.

DISCUSSION

It is unclear why eggs were found after the first three removals but after none of the later ones. This result may be due to some trivial factor such as continued growth of vegetation as time passed making it more difficult to find eggs laid in the water or on the ground.

Holcomb (1971) found that Red-winged Blackbirds continued to lay normal sized clutches in each of 11 nests from which he removed all eggs during laying. Thus egg loss alone does not normally precipitate parasitism, which is the reason I chose to remove entire nests rather than eggs only. Although my sample size is only nine individuals, it is sufficient to show that most females in the population I studied do not lay parasitically after their nest is destroyed, i.e., the 95% confidence interval for the percentage of females that do not lay parasitically is 66% to 100%. The lack of parasitism in my experimental study agrees with recent nonmanipulative studies. Gibbs et al. (1990) analyzed hypervariable DNA markers and found no parasitism in Ontario. Harms et al. (1991) applied criteria similar to mine and detected parasitism in only 0.4% (34) of 7,805 Red-winged Blackbird nests in Washington. The latter authors found no definite association between nest destruction and the rare cases of parasitism. It is clear from all three studies that Red-winged Blackbirds rarely parasitize conspecifics even when doing so apparently would make the best of a bad situation. Similarly, intraspecific parasitism is rare in two other colonial icterine species that experience nest loss during laying and that often nest with or near Red-winged Blackbirds (Harms et al. 1991, Lyon et al. 1992).

My experiments had the potential to provide support for the Hamilton-Orians hypothesis but instead argue against it, at least for the Red-winged Blackbird because this species does not resort to parasitism when it loses its nest during laying. However, my data are insufficient to invalidate the hypothesis because interspecific parasitism might start with rare individuals that switch to parasitism when their nests are destroyed during laying. But the data have clearer biological significance as regards intraspecific parasitism. My data and Holcomb's show that Red-winged Blackbirds that lose their eggs or entire nests while laying rarely, if ever, choose what seems to be the adaptive option of laying in the nest of a conspecific. This is a striking result in light of the prevalence of intraspecific parasitism, especially since Red-winged Blackbirds are colonial as are many of the species in which conspecifics are commonly parasitized (MacWhirter 1989, Rohwer and Freeman 1989).

Three other manipulative studies have tried to induce parasitism by nest destruction but all involved species known to practice intraspecific parasitism. Two studies of the European Starling (*Sturnus vularis*) found that most affected females deposited one or more subsequent eggs parasitically (Feare 1991, Stouffer and Power 1991). Similarly, nest destruction during laying caused most White-fronted Bee-eaters (*Merops bullockoides*) to attempt to lay in other nests (Emlen and Wrege 1986).

Rohwer and Freeman (1989) suggested that intraspecific parasitism is more common in precocial than in altricial birds because it is much more costly to the latter, which has resulted in the evolution of stronger host defenses in altricial species. If this hypothesis applies to Red-winged Blackbirds, they should show effective defenses against parasitism. One such defense against intraspecific parasitism is to reject dissimilar eggs (Freeman 1988). Red-winged Blackbirds nearly always accept nonmimetic cowbird eggs regardless of whether their clutches contain one of these eggs and several of their own (Rothstein 1975, Ortega and Cruz 1988) or are made up mostly or entirely of cowbird eggs (Rothstein 1982).

A defense shown by several altricial species in which intraspecific parasitism is common is to remove eggs present at the start of laying (Emlen and Wrege 1986, Stouffer et al. 1987, Brown and Brown 1989). However, this defense is rare or absent in blackbirds since it was shown by none of 15 Connecticut birds that I tested. Similarly, each of 13 females in Nebraska laid normal clutches and accepted single Red-winged Blackbird eggs placed in empty nests (Holcomb 1971) as did 85% of 27 females in Colorado that received Red-winged Blackbird-sized eggs (Ortega and Cruz 1988). But acceptance was more likely in these latter studies since the eggs added to empty nests were either conspecific ones or eggs mimetic in at least size whereas most (11 of 15) empty nests in my study received cowbird eggs which are nonmimetic as regards both size and coloration (Rothstein 1975).

Female Red-winged Blackbirds defend an area around their nest sites against other females (Searcy 1986). Although females are not truly territorial (Searcy 1988, Yasukawa et al. 1992), this nest defense could lessen the likelihood of parasitism. However, parasitism is common even in colonial species in which nest guarding occurs (Emlen and Wrege 1986, Møller 1987, Brown and Brown 1989). Furthermore, Red-winged Blackbirds often feed away from their nests (Harms et al. 1991) which would provide opportunities for parasitism. Overall, there is no evidence that evolved host defenses restrict the occurrence of intraspecific parasitism in these blackbirds and Sorenson (1992) has argued that the Rohwer-Freeman hypothesis is circular because an absence of intraspecific parasitism would provide no selection for the host defenses that are supposed to forestall parasitism.

Lyon et al. (1992) argued that indeterminate laying (Kennedy 1991) should facilitate parasitism by females that also tend their own nest. However, parasitism in response to nest loss, as in my experiment, should be facilitated by determinate laying whose inherent inflexibility should make it difficult for a bird to stop laying until its clutch is completed. It is likely that females I experimented on renested but this does not explain their failure to lay parasitically the "physiologically committed" egg that would have been the second one in the nest I removed. This is so because no new nests were built in time to receive such second eggs.

There may be unknown constraints that have selected against parasitic laying by Red-winged Blackbirds because evidence presented here shows that it fails to occur even when females are forced to waste eggs by laying them outside of any nest. Harms et al. (1991) suggested that females that experience nest loss during laying might resorb ovulated eggs. As already stated, this seems improbable in my study. Nevertheless, if females resorb ovulated eggs after nest destruction, it would further indicate that parasitism is avoided. I suggest that parasitism is rare to absent in Red-winged Blackbirds because it incurs costs that outweigh its potential benefits as parasitic eggs have relatively low success rates even in some species with high rates of intraspecific parasitism (Emlen and Wrege 1986, Evans 1988). A possible cost of parasitic laying is a risk of injury in a fight with the host female. In addition, a female caught laying parasitically might suffer a detriment in future interactions with its intended host, who is likely to be on an adjacent territory, as Red-winged Blackbirds appear to derive benefits from breeding near familiar neighbors (Beletsky and Orians 1989). Lastly, Red-winged Blackbirds that must lay an egg but have no nest in which to deposit it may often eat their egg (Harms et al. 1991), as do captive cowbirds (Dufty 1983). In such cases, the energy and materials recovered from an eaten egg may provide more benefits than attempting to lay the egg parasitically.

Determining how other species respond to nest removal experiments might reveal trends that elucidate constraints on intraspecific parasitism. In particular, it would be especially interesting to determine whether nest removal also fails to elicit parasitism in other species in which intraspecific parasitism is known to be rare. If parasitism following experimental nest loss occurs only in species that have high rates of naturally occuring parasitism, as the data suggest (this study, Emlen and Wrege 1986, Feare 1991, Stouffer and Power 1991), then it is likely that some factor other than or in addition to nest loss is necessary for the evolution of intraspecific and possibly interspecific parasitism.

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