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Costs to Northern Orioles of Puncture-ejecting Parasitic Cowbird Eggs from their Nests

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The brood parasitic *Molothrus* cowbirds lay eggs with shells that are more than 30% thicker than would be predicted from their volume (Hoy and Ottow 1964, Blankespoor et al. 1982, Spaw and Rohwer 1987). Picman (1989) has shown that two special features—the thick shells and spherical shape—of the eggs of Brown-headed Cowbirds (*Molothrus ater*) contribute about equally in making their eggs about twice as strong as those of other icterids. Three hypotheses—resistance to laying damage (Lack 1968), resistance to accidental damage by the attending host (Blankespoor et al. 1982), and resistance to puncture-ejection (Spaw and Roh-

wer 1987)—have been proposed to explain the unusually strong shells of the eggs of some parasitic cuckoos and of the *Molothrus* cowbirds. Resistance to damage at laying may be important to cuckoos that parasitize hosts with very small nests. In such cases cuckoos sometimes drop their eggs into the hosts' nests from an elevated position. Damage to the hosts' eggs, but not to the strong-shelled cuckoo eggs, has been reported in such layings (e.g. Gaston 1976).

Molothrus cowbirds almost always parasitize hosts whose nests permit the female cowbird to settle fully into them before laying. Neither the accounts of cow-

bird layings nor inspections of large samples of eggs in parasitized and unparasitized nests suggest resistance to laying damage as a reasonable explanation for the unusual strength of cowbird eggshells (Spaw and Rohwer 1987). The hypothesis of resistance to accidental damage by the attending host has been critiqued (Spaw and Rohwer 1987) and need not be reconsidered here.

Resistance to puncture-ejections seems the most plausible of these hypotheses. Many North American birds eject Brown-headed Cowbird eggs (Rothstein 1975). In general, species that eject cowbird eggs have larger bills than accepters (Rohwer and Spaw 1988, Ortega and Cruz 1988, Rothstein 1975), and most ejectors remove cowbird eggs by grasping the whole, undamaged egg between their mandibles to remove it from the nest (Rothstein 1975, Rohwer and Spaw 1988). The hypothesis of resisting puncture-ejections assumes that small birds cannot grasp cowbird eggs without first piercing the shells and proposes that the unusually strong shells of cowbird eggs resist such punctures (Spaw and Rohwer 1987, Rohwer and Spaw 1988).

This hypothesis implies that ancestral cowbird eggs of varying shell thickness and shape were deposited in the nests of various puncture-ejectors. In some host lineages, individuals were unable to puncture cowbird eggs with thicker-than-normal shells or rounder-than-normal shape, which led to stronger-shelled eggs. Stronger shells should have continued to confer a selective advantage as additional host species, which previously had been successful as puncture-ejectors, became unable to puncture cowbird eggs of still greater shell strength. The counter adaptation of hosts to evolve sharper bills seems unlikely because changes in bill morphology may have been constrained by foraging adaptations.

It is important to emphasize that, according to the hypothesis of resistance to puncture ejections, shell strength increased only because of the higher egg survival conferred on those cowbird lineages that produced eggs with stronger shells. But these increases in shell strength have important evolutionary consequences in the host community. Hosts capable of puncturing the strong shells of cowbird eggs will not benefit from doing so if the cost of puncture-ejection exceeds the costs of accepting cowbird eggs and rearing cowbird chicks that hatch. The principal cost of puncture-ejection is presumably egg breakage caused by the host's bill or the cowbird's egg striking host eggs when pecks fail to puncture the cowbird egg. After cowbird eggs became harder to puncture, hosts that previously had been ejectors of ancestral cowbird eggs may have become accepters of the new, stronger cowbird eggs, providing that attempts to puncture them resulted in excessive damage to the hosts' own eggs (Spaw and Rohwer 1987, Rohwer and Spaw 1988).

Documenting the direct benefit of stronger egg-

shells would require that some, presumably small and blunt-billed, hosts were unable to puncture cowbird eggs for ejection. As the costs of failed puncture-attempts should select against such behavior, direct observation of such costs becomes impossible. Our recourse was to determine costs of grasp- and puncture-ejections and to estimate if puncture-ejecting cowbird eggs is more costly than puncture-ejecting eggs of normal shape and shell thickness. If the puncture-ejection of cowbird eggs is more costly than either grasp-ejection of cowbird eggs or puncture-ejection of normal eggs, then some hosts might accept cowbird eggs because the costs of puncture-ejection outweigh the cost of acceptance.

At present, only the Northern Oriole (*Icterus galbula*) is well established as a puncture-ejector of Brown-headed Cowbird eggs. Eggs are grasped for ejection by being spiked on an open beak (Rothstein 1977; pers. obs.). We tested the prediction that puncture-ejections lead to more damage when the egg being removed is strong-shelled (the hypothesized "derived" condition represented by present-day cowbirds) than when the egg being removed is of normal shape and shell thickness (the hypothesized "ancestral" condition of the *Molothrus* cowbird lineage). This test does not evaluate whether or not acceptance or puncture-ejection is favored in orioles because we do not yet know the cost of rearing cowbird chicks. We also tested the assumption that grasp-ejections result in little damage to the host's own eggs when the host is large enough to remove cowbird eggs by grasping the whole undamaged egg. We used Western Kingbirds (*Tyrannus verticalis*) and American Robins (*Turdus migratorius*) as representative grasp-ejectors (Rothstein 1975; pers. obs.).

Brown-headed Cowbird eggs were obtained for these experiments by removing them from nests of various hosts (primarily Red-winged Blackbirds, *Agelaius phoeniceus*, and Brewer's Blackbirds, *Euphagus cyanocephalus*). To represent "ancestral" cowbird eggs we used the eggs of Cliff Swallows (*Hirundo pyrrhonota*). Although the size ranges of Cliff Swallow eggs and cowbird eggs overlap, on average, Cliff Swallow eggs are smaller than the eggs of the cowbird race found in eastern Washington. (Cliff Swallow: mean egg length 20.3 mm, range 17.3-22.9; mean breadth 13.9 mm, range 12.7-14.2 [Bent 1942: 463]. Cowbird: mean length 21.8 mm, range 19.8-25.4; mean breadth 16.8 mm, range 15.2-18.0 [Bent 1958: 451].) As Picman (1989) has established, cowbird eggs are also more spherical in shape; the length/breadth ratio for the above measurements was 1.30 for cowbird eggs and 1.46 for Cliff Swallow eggs. We used Cliff Swallow eggs because they were readily available and were sufficiently different from oriole eggs that we did not have to paint them to cause them to be ejected. Because shell thinning accompanies development, eggs in advanced stages of incubation were not added to any of our experimental nests. We considered eggs

TABLE 1. Damage (or lack thereof) to host eggs after host's ejection of a single introduced egg.

Category	Nests with host-egg damage	Nests without host-egg damage	<i>P</i> ^a
Puncture-ejection by Northern Oriole of swallow egg (weak shell)	1	14	0.02
Puncture-ejection by Northern Oriole of cowbird egg (strong shell)	13	20	0.02
Grasp-ejection by robin or kingbird of cowbird egg (strong shell)	0	9	

^a One-tailed Fisher's Exact test.

to be fresh enough for our experiments if they sank rather than floated in water (Hays and LeCroy 1971).

Our fieldwork was conducted from mid-May until late June in 1984 and 1985 in Douglas, Grant, and Okanogan counties, Washington. Nests were reached using a guyed extension ladder (Rohwer 1988) and were included in our study if they contained one or more oriole eggs. Prior to our egg additions, the host eggs were removed from each nest, individually numbered, and examined carefully for cracks, dents, and punctures. Any damage that had occurred prior to our experiments was circled lightly in pencil so it could be excluded from our evaluation of damage following ejections. Then the host eggs, together with an additional "parasitic" egg, were returned to the nest. Of 57 nests (Table 1), 49 were rechecked one day after being experimentally parasitized; wind and time constraints caused the remaining 8 nests to be rechecked 2-3 days (mean = 2.3 days) after being parasitized. After the experimental egg was ejected, we reexamined the host eggs and recorded the presence or absence of additional damage to individual eggs.

Orioles ejected 15 experimental Cliff Swallow eggs (our hypothesized "ancestral" weak-shelled condition of cowbird eggs) and 33 experimental Brown-headed Cowbird eggs (Table 1). After the ejections of Cliff Swallow eggs, we found no additional cracks or punctures to any oriole eggs still in the nests. In the 33 ejections of cowbird eggs, we found 12 oriole eggs (in 12 nests) with additional damage. At two nests, one parasitized with a Cliff Swallow egg and one with a cowbird egg, one and two oriole eggs (respectively) were missing when we reinspected them two days later. To be conservative in our comparison of the costs of puncture-ejecting cowbird and swallow eggs, we assumed that the missing host eggs were damaged during the host's ejection of our parasitic egg and later removed by the host. When so treated, significantly more damage to oriole eggs occurred with the ejection of cowbird eggs than with the ejection of swallow eggs (Table 1; one-tailed Fisher's Exact $P = 0.02$). Omitting these two nests or counting them as cases of no damage (as if cowbirds or predators had removed the missing eggs) increases the one-tailed significance levels to $P = 0.005$. Considering all 33 ejections of cowbird eggs and the total of 15 oriole

eggs lost or damaged, we estimate that 0.45 oriole eggs were lost or damaged for every cowbird egg ejected.

We propose that the strong shells of cowbird eggs increase the cost of puncture-ejections primarily because the host's bill or the cowbird egg itself is deflected into the host's own eggs. Damage in a few cases was subtle and easiest to detect when the shell became opaque around the tiny puncture or crack as a consequence of local dehydration. Although some of the least damaged eggs later hatched, at least 50% of all damaged eggs that we continued to observe failed to hatch. Unfortunately, nest failures and additional damage caused by natural cowbird parasitism made it impossible to conduct our analysis on the basis of hatching failures. We observed the ejections of cowbird eggs at two nests and found little or no spillage of egg contents upon reinspection of these nests. After being spiked, both of these "parasitic" eggs were removed so rapidly that spillage sufficient to stick any of the oriole's own eggs to the nest lining seemed unlikely.

Because Cliff Swallow eggs are slightly smaller than cowbird eggs, shell strength, rather than egg size, may cause the damage we found associated with the puncture-ejection of cowbird eggs (Rothstein pers. comm.). However, our experiment could have failed to show more damage during ejection of cowbird eggs than Cliff Swallow eggs. Had this been the result, our hypothesis that the strong shells of cowbird eggs may contribute to the evolution of acceptance of cowbird eggs by raising the cost of puncture-ejections would be less tenable.

The low cost of grasp-ejections was even more dramatic. No host egg at any of the Western Kingbird ($n = 7$) or American Robin ($n = 2$) nests from which cowbird eggs were ejected showed any additional damage (Table 1; Fisher's Exact $P = 0.02$). In a much larger set of observations that involved mostly artificial eggs, only five cases of missing or damaged eggs occurred in 190 grasp-ejections involving six host species (Rothstein 1976: 635). Thus, puncture-ejection seems more costly than grasp-ejection and probably evolves only when bill size or other constraints prevent grasp-ejection. The bills of Northern Orioles are smaller than those of any known grasp-ejector (Rohwer and Spaw 1988).

The pendulant nests of Northern Orioles are deeper than the nests of similar sized, open-nesting passerines, and part of the damage orioles inflicted on their own eggs when ejecting cowbird eggs may have been a consequence of the female "up-ending" to puncture the cowbird egg (Rothstein 1977). To evaluate this possibility, we measured *nest depth* as the vertical distance from the floor of the cup to the nest's lowest point of attachment. In those nests where orioles inflicted damage to their own eggs during ejection of a cowbird egg, the mean nest depth was 115.8 mm ($n = 13$; $SD = 21.4$); where no damage was inflicted mean depth was 127.8 mm ($n = 20$; $SD = 32.8$). The direction of this nonsignificant difference ($P > 0.2$; t -test) is opposite what would be expected if nest depth were a contributing cause of damage. The mean depth for the 15 nests from which swallow eggs were ejected was 118.6 mm ($SD = 19.6$), not significantly deeper than those nests from which ejection of cowbird eggs resulted in damage.

Before these experiments, we presumed that the probability of an oriole damaging some of its own eggs in puncture-ejecting a cowbird egg would increase with the number of oriole eggs present in the nest. The nonsignificant trend was otherwise: ejections of cowbird eggs that resulted in damage were from nests with a mean of 3.2 ($SD = 1.63$) host eggs while those that resulted in no damage were from nests with a mean of 3.8 ($SD = 1.16$) host eggs (2×2 median test; one-tailed Fisher's Exact $P = 0.39$). An average of 4.1 ($SD = 1.00$) eggs were present in the nests to which swallow eggs were added, a value statistically indistinguishable from that for nests from which ejection of cowbird eggs resulted in damage (2×2 median test; one-tailed Fisher's Exact $P = 0.29$). Thus, our results cannot be explained as a consequence of differing numbers of eggs available for the oriole's bill to strike.

Northern Orioles are large relative to the most frequently used hosts of the Brown-headed Cowbird. Orioles have exceptionally sharp beaks and lay larger eggs than most cowbird hosts (Friedmann et al. 1977, Rothstein 1977). Furthermore, Northern Orioles also lay eggs that have unusually thick shells for their size (Spaw and Rohwer 1987). All of these features probably minimize the costs of puncture-ejections. Smaller hosts lay smaller, more fragile eggs and usually have bills less well suited for puncture-ejecting cowbird eggs. For such hosts, puncture-ejection would surely result in much more breakage of their own eggs. However, smaller hosts will also experience higher rearing costs because cowbird chicks tend to outcompete the chicks of small hosts. The general absence of puncture-ejection among the hosts of Brown-headed Cowbirds suggests that its costs exceed the costs of acceptance. Such an argument assumes that puncture-ejection is not unduly difficult to evolve. This assumption is supported by the fact that various species of wrens remove the eggs of competitors by puncture-

ejection (Picman 1980) and that several European passerines, smaller than Northern Orioles, are now known to puncture-eject the thick-shelled eggs of the Common Cuckoo (*Cuculus canorus*) (Røskaft unpubl., Davies and Brooke 1988).

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Early Nest Departure Does Not Improve the Survival of Lapland Longspur Chicks

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In birds, the scattering of broods from the nest site before the chicks are independent (i.e. *brood dispersal*) is usually thought to reduce losses due to nest predation (Lack 1968, Ricklefs 1969). A variety of arguments have been presented to support this assumption. First, nest predation is usually identified as the major source of mortality in avian life histories (Lack 1954). Thus, any trait that reduces the amount of time that chicks spend in the nest should increase survival. Second, in almost all bird species, offspring leave the nest before they are fully developed and thus require further parental care. Although in some species further development involves only learning by the young, in most species there is also a period of physical growth after the young leave the nest (Martin 1987 and references therein). Both the premature nest departure and the fact that chicks move well away from the nest site as soon as they are able indicate that the nest may be a relatively dangerous site. Third, in ground-nesting birds, which tend to suffer a higher risk of nest predation than either tree- or hole-nesters (Ricklefs 1969, Best and Stauffer 1980, Loiselle and Hoppes 1983, Wilcove 1985), chicks leave the nest sooner, everything else being equal.

Although the logic of these arguments seems clear, few studies have presented sufficient data that would allow direct comparison of the survival of broods during the periods of parental care before and after nest departure (Nolan 1978, Dhondt 1979, Ebenmann and Karlsson 1984, Sullivan 1989). We examined the survival rates of Lapland Longspur (*Calcarius lapponicus*) chicks both before and after nest departure to test the proposition that brood dispersal improves chick survival. Maher (1964), in particular, argued that the relatively early nest departure in this species was a

consequence of predation pressure. Moreover, Williamson and Emison (1971) felt that the most plausible explanation for a 2-3 day difference in nestling periods in two longspur populations in Alaska was the difference in predation pressure. Also, chicks of the closely related Snow Bunting (*Plectrophenax nivalis*) remain in their nests about 4 days longer than longspurs and are thought to suffer less nest predation because they nest in rock crevices whereas longspurs nest in exposed cups on the open tundra (Lyon and Montgomerie 1987). This interspecific difference in the timing of nest departure is independent of size and developmental rates (Maher 1964) and therefore seems explicable only as a behavioral response to the risk of predation.

We collected data in June and July of 1981 and 1982 at Sarcpa Lake, Melville Peninsula, Northwest Territories, Canada, as part of a study on the effects of brood dispersal on the foraging behavior of parents (McLaughlin and Montgomerie 1989). We observed 7 broods (34 chicks) in 1981 and 10 broods (45 chicks) in 1982. Nests were checked at least once every other day during the 8-9 day nestling period. Nestlings were color-banded at age 6-8 days so that they could be individually identified. After nest departure, we searched for dispersed chicks, and we recorded the location and identity of each one encountered. Because these birds were easy to observe on the open tundra, we were often able to follow parents on their foraging itineraries and locate all of the young that they fed. Soon after nest departure (8-9 days after hatching) parents divided their broods into two separate units (each tended by a single parent) until independence, ca. 23 days after hatching or 14-15 days after nest departure (McLaughlin and Montgomerie 1985). By 18 days after hatching (9-10 days after nest departure), young longspurs began feeding themselves and were more mobile. Because they were increasingly difficult to locate as they became more mobile, we restricted our analyses to chicks ≤ 17 days

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