SHORT COMMUNICATIONS

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RESPONSES OF BIRDS TO BROKEN EGGS IN THEIR NESTS[1]

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Abstract. We tested the responses of two bird species which nest on unmovable substrates (e.g., cavities and walls) to simulated and actual egg damage in their nest. Tree Swallows (*Tachycineta bicolor*) and Barn Swallows (*Hirundo rustica*) removed broken eggs and continued to incubate the rest of their clutch, but response times took up to 8 days, and observed rejection rates were lower than reported for some other passerines. Collectively, these data and other studies suggest that broken eggs represent a continuing selection pressure to which all birds respond, although there appears to be some variability among species in the strength and speed of the response to damaged eggs.

Key words: Barn Swallow, egg recognition, Hirundo rustica, *nesting substrate,* Tachycineta bicolor, *Tree Swallow.*

For many birds, the hatching success of a clutch largely determines their reproductive output for that breeding season. Selection should favor birds that recognize and respond to any factors that might reduce hatching success (Rothstein 1975a, 1975b). One such factor is egg damage (Kemal and Rothstein 1988), because damaged eggs in bird nests are less likely to hatch (Carey 1986) and may affect the hatching success of the remainder of the clutch by attracting predators (Kemal and Rothstein 1988). Thus, selection should favor parental recognition and removal of eggs with broken shells. Damage to eggs in bird nests may occur from a variety of sources, including freezing temperatures, competition between females for nest sites, predation, accidental damage from non-predators, and inter- and intraspecific nest parasitism.

Ejection of damaged eggs by parent birds has been reported for numerous species (Kemal and Rothstein 1988). These authors also suggested that passerines which nest on unmovable substrates are less likely to reject damaged eggs, presumably because egg damage resulting from nest movement or predation in these nest sites would be less frequent than for nests on movable substrates. Hence, selection for recognition of damaged eggs for birds nesting on unmovable substrates may be less intense. However, not all birds that nest on unmovable substrates experience lower rates of egg damage. For example, cavity-nesting birds' nests do not move, but these birds may experience egg damage from many of the same factors mentioned above (Lombardo 1988). Thus, we predicted that birds nesting on unmovable substrates should respond to broken eggs in their nests like those birds nesting on movable substrates.

In this paper, we report on the responses of Tree Swallows *Tachycineta bicolor* and Barn Swallows *Hirundo rustica,* both species that nest on unmovable substrates, to damaged eggs in their nests. Our first objective was to determine whether these species respond to broken eggs as has been reported for birds nesting on movable substrates (Kemal and Rothstein 1988). Our second objective was to examine whether responses to simulated broken eggs differed from responses to eggs that were actually broken.

METHODS

Most nest experiments were conducted in 1996 and 1997 on swallows nesting at the Queen's University Biological Station (QUBS), eastern Ontario, Canada (44°34′N, 76°20′W), whereas the others were carried out at the Mallory farm, 20 km south of the first site (44°27′N, 76°11′W). All Tree Swallow experiments were on birds nesting in nest boxes distributed singly on aluminum poles and fence posts in hay fields and along roadsides. Barn Swallow nests were located in a boat house at QUBS, and were in garages and barns at the Mallory farm. Incubation stage of Tree and Barn Swallow nests at QUBS was known from concurrent studies.

For nest experiments, we modified the procedure of Kemal and Rothstein (1988). We assigned each nest to one of three categories for experimental manipulation: (1) two "flat" eggs (simulated subtle-damage nests), (2) one "flat" egg and one "angle" egg (simulated major-damage nests), and (3) one "flat" egg and one "hole" egg (actual damage nests). For subtle damage nests, we selected two eggs from each nest and attached a small (approximately 5 × 3 mm) piece of a white, chicken egg-shell flat against the side of each of the experimental eggs ("flat" eggs) with rapidly-drying glue from a hot glue gun. Once dry, the at-

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TABLE 1. Responses of Tree Swallows and Barn Swallows to eggs with varying degrees of damage. Experimental nests contained subtle-damage eggs (two eggs with flat pieces of shell; $n = 11$ for Tree Swallows and $n = 5$ for Barn Swallows), simulated damage (one egg with a flat piece and one egg with an angled piece of shell; $n = 16$ and 11, respectively), and actual damage (one egg with a flat piece of shell and one egg with a hole in it; $n = 18$ and 10, respectively). Eggs within these nests were categorized as normal (no manipulation), flat (a flat piece of shell was attached), angled (an angled piece of shell was attached), or hole (a 2-mm hole was poked through the eggshell).

	Simulated subtle-damage eggs		Simulated major-damage eggs			Actual damage eggs		
Response in 24 hours	Normal	Flat	Normal	Flat	Angled	Normal	Flat	Hole
Tree Swallow								
n eggs removed	0	2	0	8	9	0	8	9
n eggs not removed	38	20	56	8	7	64	10	9
Barn Swallow								
n eggs removed	0	8	0	5	7	0	3	6
n eggs not removed	15	2	36	6	4	32	7	4

tached shell was raised approximately 1 mm above the surface of the rest of the egg (note that this is "higher" than the procedure performed by Kemal and Rothstein (1988), and thus may represent a stronger stimulus). For simulated major damage nests, we again used two eggs from each nest, and attached one small piece of egg shell flat against one egg as above, but the second egg received a piece of eggshell which was glued at a 45° angle ("angle" eggs), protruding about 3 mm out from the side of the egg. For actual-damage nests, we selected two eggs from the nest and glued one eggshell fragment on flat against the side, but on the other egg we poked a small (2 mm diameter) hole ("hole" eggs) such that the liquid egg-contents could be seen. These eggs were replaced with the hole pointed up so the liquid was not leaking from the egg. With the above procedures, the egg receiving the flat attachment in each nest served as an in-nest control for the real or simulated damage to the other egg (Kemal and Rothstein 1988). Also, the nests receiving two flat attachments served as controls for the other nests. The total duration of egg manipulations required about 10 min, and females usually remained nearby or returned as we were leaving the nest.

Eggs were manipulated anywhere between day 2 to day 8 of incubation for Tree Swallows, and between day 2 and day 10 of incubation for Barn Swallows (typical incubation period for both species 13–16 days). All nests were revisited 24 hr later (in some cases earlier than 24 hr and then again at 24 hr), and the number of experimental eggs remaining in the nest was recorded. Because Tree Swallow nests at QUBS also were used in other studies, they were visited approximately once every two days until hatch.

RESULTS

GENERAL RESPONSES

Tree Swallow females nesting at QUBS were in their first to seventh breeding season, but ages of Barn Swallow females were unknown. Clutch sizes of both species ranged from 4 to 7 eggs. For both species, birds that responded to broken eggs in their nest did so by removing the egg from the nest or nest box; no eggshell attachments were snapped off of the egg, and no broken eggs were buried in the nest material or placed in the nest box but outside of the nest cup. Response times ranged from < 3 hr to 8 days, although we restricted statistical analyses to responses that occurred within 24 hr. No nests were abandoned due to our manipulations.

RESPONSES TO EGG DAMAGE

For Tree Swallows, 45 nests containing 248 eggs were used, in which 90 eggs were manipulated (Table 1). In these trials, eggs were removed from more nests with simulated major damage or actual damage (18 of 34, 53%) compared to nests with simulated subtle damage (1 of 11, 9%) within 24 hr (Fisher exact test, $P < 0.02$). Moreover, eggs were removed by Tree Swallows 3–8 days after manipulation from 6 of the 16 nests (38%) where there was no response in 24 hr. For all nests, no unmanipulated, "normal" eggs were ever removed.

For Barn Swallows, 26 nests containing 135 eggs were used, in which 52 eggs were manipulated (Table 1). Barn Swallows removed eggs in similar frequencies from subtle damage nests (80%, 4 of 5) and nests with simulated major or actual damage (62%, 13 of 21; Fisher exact test, $P = 0.4$), indicating that nests containing eggs with any form of manipulation had those eggs removed. All responses to damaged eggs by Barn Swallows were within 24 hr.

RESPONSES TO SIMULATED AND ACTUAL DAMAGE

Tree Swallows removed 40% (36 of 90) of all manipulated eggs in nests within 24 hr. The simulated major damage (shell fragment glued at an angle) and actual damage (a hole) to eggs in nests elicited similar responses from Tree Swallows; damaged eggs were removed at 56% of nests (9 of 16) with simulated major damage and at 50% of nests (9 of 18) with actual damage (Table 1; Fisher exact test, $P = 0.5$). At 89% of Tree Swallow nests (16 of 18) where simulated major or actual damaged eggs were ejected, swallows also ejected the subtle damage egg with the flat piece of shell (Table 1). The fact that these eggs were removed at only 9% (1 of 11) of subtle damage nests but 47% of nests with simulated major or actual damaged eggs (16 of 34; Fisher exact test, $P = 0.03$) suggests that the occurrence of a major damage egg caused the female to examine the rest of her clutch and remove those with any apparent damage.

Barn Swallows removed 56% (29 of 52) of all manipulated eggs in nests. In subtle damage nests, 80% (8 of 10) of manipulated eggs were removed, even though these eggs all had shell pieces glued flat against the real egg. In nests with simulated major or actual damage, 8 of the eggs with a piece of shell attached flat to the side of the egg also were removed from the 13 nests (62%) where the egg with an angled fragment or hole was removed, a proportion similar to subtle damage nests (Fisher exact test, $P = 0.4$). Overall, there was no difference in removal of manipulated eggs at subtle damage nests (80%) and manipulated eggs at nests with simulated major or actual damage (50%; 21 of 42 eggs; Fisher exact test, $P = 0.16$).

DISCUSSION

Kemal and Rothstein (1988) found that certain bird species nesting on unmovable substrates did not remove simulated broken eggs from their nests. Because birds nesting on these substrates typically experience lower predation and probably less natural damage to eggs from jostling due to nest movement, they postulated that their nest location may have reduced the selective pressure for these species to recognize broken eggs compared to birds nesting on mobile substrates. Our data provide some evidence that part of this hypothesis can be rejected. Tree Swallows removed 40% and Barn Swallows removed 56% of all eggs manipulated in nests, compared to the complete lack of removal of any unmanipulated eggs. Hence, our data indicate that both of these species recognize and respond to broken eggs in their nest by removing them, although at lower rejection rates than observed for Red-winged Blackbirds (*Agelaius phoeniceus,* 83%; Kemal and Rothstein 1988). Therefore, our results are consistent with the hypothesis that selection pressures exist for removing broken eggs even when nests are on unmovable substrates, and thus we support Kemal and Rothstein's (1988) contention that rejection of broken eggs represents an ancestral, universal, and continuing selection pressure.

Although most species studied appear to remove broken eggs from their nest, methods of responding to these eggs may differ, and there is clear variability in responses among individuals within a species. For example, Kemal and Rothstein (1988) found that all egg removals occurred within 24 hr for Red-winged Blackbirds, but we observed responses occurring between 3 hr and 8 days after egg manipulations for swallows, with one quarter of damaged Tree Swallow eggs removed more than 24 hr after the damage was evident. We suspect that response times by females vary because: (1) females may vary considerably in their ability to detect broken eggs, (2) females may vary in their ability (or experience) in removing broken eggs, or (3) other external factors such as predation pressure may influence the female's assessment of the level of risk posed by the broken egg and hence her need to remove it. At present there are no data to test any of these possibilities.

Data from our study suggest that the presence of an egg with major damage in the clutch apparently caused the female to examine the rest of her eggs more closely. We arrived at this conclusion because the subtle damage eggs were removed more often from nests also containing an egg with major or real damage than from nests without these eggs, although sample sizes were small. In contrast, Kemal and Rothstein (1988) found no difference in removal of control eggs from nests with or without eggs exhibiting damage. Hence, they concluded that the lack of response to the control egg suggested that the female's response to each egg was an independent event. Our results suggest that this conclusion does not apply to all species.

Almost all species examined appear to recognize damaged eggs in their nests (Kemal and Rothstein 1988), although the mechanism by which egg damage is recognized and the factors that dictate female response times to broken eggs are unknown. We can assume that our ability to reliably survey the frequency of naturally damaged eggs in the wild is very limited, because it appears that birds usually remove these from their nest quickly. Nonetheless, it would be useful for researchers to report these types of observations so that a baseline of the frequency of natural egg damage can be established. Such a baseline would be an important measure against which the influence of external factors (e.g., cowbird parasitism, pollutant effects, nest disturbance by humans) could be compared.

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