

PREDATION ON JAPANESE QUAIL VS. HOUSE SPARROW EGGS IN ARTIFICIAL NESTS: SMALL EGGS REVEAL SMALL PREDATORS¹

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Abstract. Nest predation studies frequently use eggs such as Japanese Quail (*Coturnix japonica*) to identify potential predators of Neotropical migrants' eggs, but such eggs may be too large or thick-shelled to identify the full complement of potential predators. We compared predation events and predators of Japanese Quail and smaller House Sparrow (*Passer domesticus*) eggs in paired, camera-monitored ground nests within edges and interiors of 40 mixed-hardwood forest stands in central Massachusetts. House Sparrow eggs were depredated significantly more than Japanese Quail eggs at both forest edges and interiors. Eleven potential predator species disturbed nests, six of which were confirmed as predators. Our use of House Sparrow eggs revealed predation by eastern chipmunks (*Tamias striatus*) and Black-capped Chickadee (*Parus atricapillus*), but not by white-footed mice (*Peromyscus leucopus*), the most abundant small mammal species in all 40 stands. Neither predator species composition (as detected by camera) nor the frequency of nest predation differed between forest edge and interior. We conclude that the egg type used in artificial nest studies affects both the predation rates and the predator species detected.

Key words: artificial nests, nest predation, *Peromyscus leucopus*, *Parus atricapillus*, predator behavior, small nest-predators, *Tamias striatus*.

INTRODUCTION

Although the importance of nest predation to our understanding of avian reproductive strategies has been recognized for over 40 years (Lack 1954, Nice 1957), identification of actual nest predators has proven difficult. Most efforts have used artificial nests, but the utility of such nests for identifying true nest predators has been questioned (Martin 1987, Storaas 1988, Major and Kendall 1996).

One of the most common objections to the use of artificial nests has been the apparent failure to identify or account for the effects of small nest-predators, which may be critical given their potentially greater relative abundance (Roper 1992, Haskell 1995). Many experimental setups may have excluded potential small predators by use of eggs that were too large or thick-shelled (Reitsma et al. 1990, Sieving and Willson 1998). Moreover, eggs as large as Japanese Quail (*Coturnix japonica*) or as small as Zebra Finch (*Taeniopygia guttata*) often do not aptly represent those of the avian species of interest and their use may lead to misinterpretation of potential nest predator behavior (Craig 1998). Unlike

Zebra Finch or Japanese Quail eggs, the eggs of House Sparrows (*Passer domesticus*) approximate the mean egg dimensions of many ground- and low-nesting Neotropical migrants and have color and markings similar to those of many small forest passerines (Harrison 1975).

After determining that captive, wild-captured white-footed mice (*Peromyscus leucopus*) were capable of breaching and consuming House Sparrow eggs in preliminary laboratory trials, we wanted to know whether these eggs, in contrast to Japanese Quail eggs, would allow us to photographically document predation by small nest-predators. Accordingly, we conducted a field study comparing predation on two egg types (Japanese Quail, hereafter "quail" and House Sparrow, hereafter "sparrow") in paired, camera-monitored ground nests. Our objectives were to determine whether predation frequency differed by egg type, who the predators of each egg type were, their depredatory behavior at the nests (focusing on small predators), and whether there were any differences between forest edge and interior locations, given that predator species and their densities may differ by habitat (Wilcove 1985, Angelstam 1986). We hypothesized that sparrow eggs would be depredated

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more frequently than quail eggs and that a more diverse guild of predators, including smaller predators, would be detected with the smaller sparrow eggs. For the purposes of this study, we defined "predation" as any activity that would destroy a viable egg; this included egg-pecking behavior that resulted in a breached egg.

METHODS

STUDY AREA

We selected 40 mature forest stands, each with an edge formed by an adjacent clearcut, from a 630-km² extensive, mixed-wood forest surrounding the Quabbin and Ware River watersheds in central Massachusetts. Managed for water quality, these watersheds are a landscape matrix of mostly continuous forest cover with a small percentage of scattered openings and agriculture. Individual stands were separated from each other by at least 0.5 km and by an average distance of 3 km. The 2–4 ha regenerating clearcuts ranged in age from 1 to 6 years old. All mature stands were at least 80 years old, at least 3 ha, and of the red oak (*Quercus rubra*)-white pine (*Pinus strobus*)-red maple (*Acer rubrum*) forest-cover type (Eyre 1980).

CAMERA-MONITORED ARTIFICIAL NEST SETS

We placed two camera-monitored sets of artificial nests, one near (5–15 m) and one far (100–120 m) from edges in each of the 40 stands. All nest sets were exposed within two weeks of each other for 12-day periods during June–July 1997. We performed a single trial per stand because the potential for learning may exist in predators (Vander Haegen and DeGraaf 1996, Wilson et al. 1998). Each nest set consisted of two aviculturists' wicker baskets, 10 cm in diameter and 6 cm deep, joined together at the rim. One nest contained a sparrow egg, the other a quail egg (160 nests total). The two egg types were put in separate nests because animal activity in a single nest containing both eggs can result in the larger, thicker-shelled quail egg breaking the sparrow egg (pers. observ.). Each nest had a miniature electronic limit switch attached inside on the nest bottom (Ball et al. 1994). Switches included an elongated aluminum actuator arm that we split and bent to hold each egg type low in the basket to prevent small animals from crawling underneath the actuator arm and tripping the camera. We painted switches flat black to eliminate white or shiny surfaces. The attached bas-



FIGURE 1. Raccoon (*Procyon lotor*) depredating nest set containing House Sparrow (*Passer domesticus*) and Japanese Quail (*Coturnix japonica*) eggs on 2 July 1997 in central Massachusetts.

kets' switches were connected to a single camera using a simple series circuit. This design activated the camera when the first of either egg type was removed from the switch (Fig. 1). The 35-mm cameras ("point-and-shoot" with 35-mm lenses [*f*/3.5] and ISO 200 color negative film) were enclosed in camouflage-painted, weatherproofed wooden boxes (Danielson et al. 1996).

Quail eggs were purchased immediately before their use and feral sparrow eggs were gathered and refrigerated in the week prior to use. Eggs were rinsed in well water and air-dried before using. Nest sets were weathered for three weeks prior to use. We wore clean rubber boots, clean cotton gloves, and placed our equipment on clean plastic drop sheets when deploying nests to minimize human scent and disturbance at the sites (Whelan et al. 1994).

Nest sets were positioned to mimic a natural passerine ground-nest (e.g., Black-and-white Warbler, *Mniotilta varia*), taking advantage of natural cover, and set flush with the surface litter. The camera cable was threaded underneath leaf litter to the camera box, which was attached to a tree bole 1–2 m from the nest set. We attached the camera boxes high enough on the tree so that any action within the nests by small animals would be photographed.

TABLE 1. Comparison of artificial nest set outcomes using two egg types, between forest edge and interior for 40 stands in central Massachusetts, June and July 1997.

	Predation			Disturbance		Neither predation nor disturbance	Total
	Both eggs	Sparrow egg only	Quail egg only	Sparrow egg only	Quail egg only		
Edge	15	8 ^a	0 ^a	7 ^a	2 ^a	8	40
Interior	12	11 ^a	2 ^a	7 ^a	5 ^a	3	40
Total	27	19	2 ^b	14	7	11	80

^a Frequencies used for two-tailed binomial tests.^b Sparrow eggs at these sets were completely covered by leaves at time of large-egg predation, as determined by photographs.

IDENTIFICATION OF PREDATION, PREDATOR SPECIES, AND ASSEMBLAGES

Nest sets were checked after a 12-day period, approximately the incubation time for small forest passerines (Rahn and Ar 1974). Eggs found out of the nest, destroyed in the nest, or missing were considered predation events. Eggs found off their trigger, but still in the nest, were considered "disturbed."

Color photographs, along with any corroborative remains of depredated eggs, were our primary means of identifying predators. In the event subsequent visits were recorded, we used only photographs representing the initial disturbance at each of the 80 nest sets. Eggshell remains alone may not indicate predator identity (Larivière 1999); we only used eggshell remains as supporting evidence to photographs and then only when the remnants retained diagnostic value. Our decisions on whether to classify an animal as an egg predator were carefully made. For example, a photograph of an eastern chipmunk (scientific names listed in Table 2) with an egg in its mouth was taken as evidence of predation, whereas a chipmunk holding an egg (that was later found depredated) was considered a predation event by that animal only if egg remains were supportive (e.g., the egg shell had a 4–8 mm diameter hole in the blunt end). Objectivity in "predator" identification was necessary because we photographed chipmunks holding eggs in their forelimbs without subsequent egg predation.

To better illustrate and analyze our comparisons between the two egg types in regard to predators, we categorized the observed predator assemblage based on their egg-type handling capabilities. We defined "large" predators as those animals capable of depredating either of our egg types, such as raccoon, and "small" predators as those animals incapable or unlikely to readily

consume or otherwise depredate quail eggs, such as white-footed mice (DeGraaf and Maier 1996).

STATISTICAL ANALYSIS

We used two-tailed binomial tests to analyze the predation and disturbance frequencies of egg type for forest edge and interior separately, using $P = 0.5$ as our null hypothesis (Zar 1996). A Wilcoxon signed-rank test using depredated egg type was used to compare outcomes between forest edge and interior nest sets for the 40 stands. Contingency tables using a chi-square statistic with appropriate continuity corrections were used to compare potential predator assemblages initially disturbing nest sets and confirmed predator assemblages detected at forest edge and interior. We performed statistical analyses using SYSTAT 7.0 for Windows, with a significance level of $P < 0.05$ for all tests.

RESULTS

EGG TYPE

Of the 80 artificial nest sets, 60% had one or both egg types depredated, 26% were disturbed, and 14% were undisturbed (Table 1). Sparrow eggs were depredated significantly more than quail eggs at both forest edge (two-tailed binomial, $P < 0.01$) and forest interior sites (two-tailed binomial, $P < 0.05$). Sparrow eggs also were disturbed more than quail eggs, but this trend was not significant at forest edge (two-tailed binomial, $P > 0.1$) and forest interior sites (two-tailed binomial, $P > 0.7$).

PREDATOR IDENTIFICATION

Eleven species, seven mammalian and four avian, comprised the assemblage of potential nest predators initially photographed at nest sets (Table 2); eastern chipmunks were most frequently detected (46%), with white-footed mice the next

TABLE 2. Number of times species photographed as initial visitors disturbing nest sets (“potential predators”) and confirmed as predators between forest edge and interior.

Species	Initial visitation			Confirmed predation		
	Edge	Interior	Total	Edge	Interior	Total
Eastern chipmunk (<i>Tamias striatus</i>)	10	16	26	4	7	11
White-footed mouse (<i>Peromyscus leucopus</i>)	5	3	8	0	0	0
Fisher (<i>Martes pennanti</i>)	3	4	7	3	4	7
Raccoon (<i>Procyon lotor</i>)	3	1	4	3	1	4
Black-capped Chickadee (<i>Poecile atricapillus</i>)	1	2	3	0	1	1
Blue Jay (<i>Cyanocitta cristata</i>)	0	2	2	0	2	2
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	1	1	2	0	0	0
Red-backed vole (<i>Clethrionomys gapperi</i>)	2	0	2	0	0	0
Porcupine (<i>Erethizon dorsatum</i>)	1	0	1	1	0	1
Flying squirrel (<i>Glaucomys</i> spp.)	1	0	1	0	0	0
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	1	0	1	0	0	0
Unidentified small bird	0	1	1	0	0	0
Unidentified small mammal	0	1	1	0	0	0
Suspected small mammal predator	—	—	—	3	3	6
Unidentified predator	—	—	—	9	7	16
Total	28	31	59	23	25	48

most frequently detected (14%). Of the 59 initial visits, 76% were by potential small predators and 24% were by potential large predator species (Table 3). We photographed more than one species of potential predator at 32% of the 59 nest sets where activity was recorded; in five cases, detecting up to three different species at a nest set site in a 12-day period.

Six predator species, four mammalian and two avian, were documented depredating artificial nest sets (Table 2); eastern chipmunks were the predominant predator (42%), with fisher the next most common predator (27%). Of 48 predation events, 25% were by small predators, 29% were by large predators, and 46% were unidentified (Table 3).

TABLE 3. Small potential predators were detected more than large potential predators as initial visitors, but accounted for approximately the same amount of confirmed predation (in parentheses) at both forest edge and interior.

	Small ^a	Large ^b	Unidenti- fied ^c	Total
Edge	21 (4)	7 (7)	— (12)	28 (23)
Interior	24 (8)	7 (7)	— (10)	31 (25)
Total	45 (12)	14 (14)	— (22)	59 (48)

^a Includes chipmunk, mouse, vole, squirrel, chickadee, towhee, warbler, unidentified small bird, and small mammal.
^b Large predators include fisher, raccoon, porcupine, and jay.
^c Unidentified predators include suspected mammal predators.

SMALL PREDATOR BEHAVIOR

Photographs of initial nest visits by eastern chipmunks depicted them disturbing quail eggs in 5 cases and sparrow eggs in 21 cases. Chipmunks were capable of holding quail eggs with their forelimbs (photographed in two cases), but we confirmed predation of this egg type by chipmunks only once, after finding the quail egg 3 m from the nest, still intact, but heavily scratched on both ends. Chipmunks were more facile at handling the sparrow eggs (Fig. 2). We photographed chipmunks holding these eggs in mouth or with forelimbs in 10 cases. When holding a sparrow egg with their forelimbs, chipmunks usually had the blunt end up, where the egg contents were often extracted through a 4–8 mm hole. We observed similar sparrow egg remains in six additional cases of predation without associated photographs, but were unable to assign responsibility to chipmunks. We have witnessed captive white-footed mice make somewhat similar excisions, so these depredations were classified as “suspected small mammal predator” (Table 2).

We detected Black-capped Chickadees three times as initial visitors to our nest sets (in all cases, they were at the sparrow egg), but we were able to confirm depredation only once. The egg had a small puncture-like hole on its side, approximately 3 mm in diameter, with some shell fragments pushed into the egg’s contents,

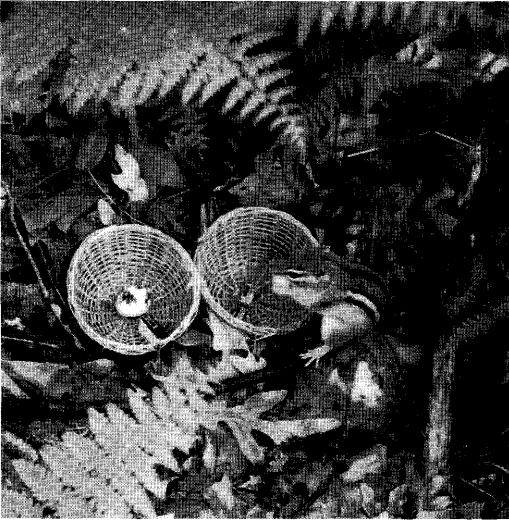


FIGURE 2. Eastern chipmunk (*Tamias striatus*) depredating only House Sparrow (*Passer domesticus*) egg at nest set on 19 June 1997.

none of which appeared to be missing. Chickadees apparently were not alarmed by our camera's operation, characteristically having multiple photographs taken while at the nest, a behavior that suggests that they repeatedly pecked at the egg.

LOCATION EFFECT

We did not detect a difference between predation events (i.e., one egg or both egg types depredated) at forest edge ($n = 23$) or interior sites ($n = 25$) for the 40 stands (Wilcoxon signed-rank, $T = 126.0$, $P > 0.9$). Likewise, we did not detect any differences between forest edge and interior sites in either the proportion of nests disturbed by potential predators initially visiting nests ($\chi^2_1 = 0.0$, $P > 0.9$) or the proportion of nests depredated by confirmed predators ($\chi^2_2 = 1.4$, $P > 0.4$) (Table 3).

DISCUSSION

Our results indicate that the size and shell-thickness of eggs used in artificial nest studies can affect predation frequency, as well as the predator species detected. This is in accordance with the observations of both Roper (1992) and Haskell (1995); artificial nest studies frequently use eggs that are too large or thick-shelled to reveal potential small nest-predators. Egg size correlates with shell thickness, breaking strength, and resistance to puncture (Romanoff and Romanoff

1949, Burley and Vadehra 1989); however, most artificial nest studies use commercially obtained quail eggs that have diet-induced thick shells to reduce handling and shipping damage. Sieving and Willson (1998) acknowledged that shell thickness greater than that in wild birds' eggs of comparable size may have accounted for their finding of no difference in predation rates between Japanese Quail eggs and much smaller buttonquail (*Turnix* spp.) eggs. We observed that smaller, feral House Sparrow eggs were depredated significantly more frequently than larger, commercially obtained Japanese Quail eggs.

The design of this study precludes our ability to report independent predation rates for either egg type because we sacrificed independence between egg types to reduce extrinsic variability. Nevertheless, subsequent observations of both egg types in 140 independent artificial nests separated by at least 70 m yielded similar results (unpubl. data); the predation rate was 64% for House Sparrow eggs ($n = 70$) and 26% for Japanese Quail eggs ($n = 70$). We conclude that the type of eggs used in artificial nest studies may bias the interpretation of both predation rates and predator identity.

Many nest predation studies have indirectly provided evidence that there may be numerous potential nest predator species in a given habitat (Reitsma et al. 1990, Leimgruber et al. 1994). We documented a total of 11 potential predator species, 6 of which were confirmed as predators. Our film records show that many of the nest sets were visited by at least three potential predator species. Of the species we classified as large predators, fisher, raccoon, porcupine, and Blue Jay have been previously documented as nest predators (DeGraaf 1995, Danielson et al. 1996, Bayne and Hobson 1997). Of the species we classified as small predators, some observers have considered eastern chipmunks as at least occasional nest predators (Pettingill 1976, Elliot 1978), whereas others have not (Reitsma et al. 1990), and Black-capped Chickadees have been documented for apparent interspecific egg-pecking behavior, but not actually destroying eggs (Picman and Belles-Isles 1988).

Eastern chipmunks, our most frequently documented nest predator, exhibited a certain facility for depredating House Sparrow eggs, as opposed to Japanese Quail eggs. Diet studies have revealed carnivorous tendencies in chipmunks, and avian remains have been observed in gut

samples (Forbes 1966, Wrazen and Svendsen 1978). In contrast, Reitsma et al. (1990) found no difference in predation rates between control plots and those from which they removed chipmunks and red squirrels (*Tamiasciurus hudsonicus*), leading them to surmise that these species were not important nest predators. Reitsma et al. acknowledged, however, that chipmunks may have had difficulty depredating the Japanese Quail eggs used in their study.

As to why sparrow eggs were not depredated in all cases where chipmunks were detected (Table 2), we offer only conjecture. Chipmunk size may have been a factor, however, we were unable to discern such differences between successful animals and those that were not. Given that photographed chipmunks often displayed alert postures, as described by Wolfe (1969), possibly the flash of the camera, the sound of the film-wind motor, or a combination of these factors may have been sufficient to drive chipmunks off.

In the only previous documentation of interspecific egg-pecking behavior by Black-capped Chickadees, Picman and Belles-Isles (1988) reported witnessing the behavior once on an artificial nest containing an unbroken Red-winged Blackbird (*Agelaius phoeniceus*) egg and detecting another six possible cases. They acknowledged that whereas egg-pecking among passerines was thought to be relatively rare, the behavior could be somewhat more common, just difficult to document. Our confirmation of egg depredation by a chickadee would have been impossible if the event had happened early in the exposure period, because it is very likely that the breached egg would have been consumed by another visitor to the site, given that many of our sites exhibited photographic evidence of more than one species' visit. Our camera-trigger mechanism was designed to trip the camera on removal of either egg, rather than the destruction of an egg by pecking (i.e., by depressing the camera trigger). Therefore, egg-pecking may have been more prevalent in this study, but we were largely unable to detect it. Refined detection techniques using small eggs and different camera triggers may result in more observations of egg depredation by small passerines.

We were surprised that we did not document predation by white-footed mice. Mice (*Peromyscus* spp.) have often been implicated as potential nest predators in earlier narrative ac-

counts (Bent 1968, Maxson and Oring 1978, Murray et al. 1983) as well as more recent nest predation studies (Hannon and Cotterill 1998, Keyser et al. 1998), and large Keen's mice (*P. keeni*) found on Triangle Island, British Columbia, have been reported to open Rhinoceros Auklet (*Cerorhinca monocerata*) eggs (Blight et al. 1999). Additionally, our preliminary laboratory trials revealed that even some juvenile, wild-captured white-footed mice were capable of breaching and consuming House Sparrow eggs. In this study, white-footed mice were the second most abundant species initially detected (14%), and detected in again as many stands with secondary photographs (taken after a predation or disturbance). Likewise, in a later study in the same study areas that assessed the relative abundance of small mammals (DeGraaf et al. 1999), white-footed mice were detected more than all other small mammal species combined and were the only species detected in all 40 stands. Nevertheless, white-footed mice were not confirmed as predators on artificial nests in this study.

There may be a number of explanations for our lack of evidence of egg predation by white-footed mice despite their abundance. First, the ability of white-footed mice to breach and completely consume our small eggs in captivity may have been aberrant behavior associated with confinement (Kavanau 1967). Second, not being confined, the mice may have only initially inflicted small breaches to the egg, as reported by Maxson and Oring (1978), rather than more substantial damage that would have been obvious in the photographs. Finally, there is the possibility that white-footed mice, a relatively small species of *Peromyscus* (Lackey et al. 1995), may not regularly depredate passerine eggs that are the size of House Sparrow eggs or larger. Based on laboratory trials that exposed white-footed mice to different egg types, we showed that the use of Zebra Finch eggs in artificial nests would result in predation by mice (DeGraaf and Maier 1996); however, even if white-footed mice are capable of depredating very small, thin-shelled eggs, they may be infrequent nest predators of most Neotropical passerine species.

Forest edge and interior may have different predator communities in some landscapes (Picman 1988). Nevertheless, we were unable to detect any differences in the distribution of either individual species or predator assemblage be-

tween forest edge and interior sites. Similarly, Heske (1995) detected no significant differences between the number of small mammals or fur-bearers at forest-farm edges and interiors in Illinois, and attributed these results to site variation, detection method shortcomings, or forest characteristics belying true forest interior. Our inability to find differences might similarly be attributed to the relatively small clearcuts that formed edges at our 40 sites within extensive forest. In other words, we may have found no differences in the diversity of predator species because sufficient landscape differences did not exist.

The species to which we attributed predation in this study were photographed depredating artificial, rather than real nests; thus, we make no claim to have documented natural rates of nest predation. The construction of these nest sets, the presence of a camera at 1–2 m distance, and the lack of parental defense afforded true passerine nests may have all affected, to various degrees, our results and observations. As an attempt to compensate for the artificiality of our setup and reduce subjective bias, we were careful in attributing predation events to individuals. Species detected at initial visits were not automatically considered predators because we discovered that our camera switches were very sensitive when used in conjunction with sparrow eggs. Nevertheless, it also is important to recognize that some of the species detected disturbing our nests, such as Eastern Towhee, may have been depredating artificial nests, but we were unable to confirm such predation during this study.

In summary, potential, small avian-nest predators were much more capable of depredating House Sparrow eggs than Japanese Quail eggs in artificial nests; thus, more predator species or their effects were detected. We quantified and confirmed the identification of smaller predator species capable of artificial nest depredation previously cited in narrative accounts. Eastern chipmunks may play a large role in Neotropical passerine ground-nest predation, but also may exhibit a high sensitivity to monitoring devices, thus reducing their apparent role as nest predators. Black-capped Chickadees, displaying interspecific egg-pecking behavior, may occasionally destroy small passerine eggs. White-footed mice may infrequently depredate passerine eggs the size of House Sparrow eggs or larger, so their

effectiveness as true nest predators is questionable. Consideration of these behaviors should lead to more successful methods of monitoring real nests and the interpretation of what is thereby observed.

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