VISUAL AND OLFACTORY ATTRIBUTES OF ARTIFICIAL NESTS

SHEILA A. RANGEN,[1] ROBERT G. CLARK, AND KEITH A. HOBSON

Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada;
and
Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada

ABSTRACT.—Artificial nests are commonly used to investigate relative rates of nest predation in birds, but several methodological considerations need to be addressed before results from natural and artificial nests can be compared. Using field and laboratory experiments, we examined responses of predators to visual and olfactory cues that were associated with wicker nests and their contents. Avian predators did not discriminate between wicker nests dipped in mud and those covered by a camouflage fabric, whereas mammalian predators showed a weak tendency to depredate camouflaged nests. Nests containing plasticine eggs were depredated more often than nests containing only quail eggs and finch eggs, although no response to number of plasticine eggs in nests was found. The higher predation of nests with plasticine eggs may have resulted because small mammals, relying on olfactory cues, comprised a large portion of the predator assemblage. Field results were supported in tests where captive deer mice (*Peromyscus maniculatus*) were attracted to assortments of egg types that included plasticine. Time required by captive deer mice to penetrate quail eggs and finch eggs versus plasticine eggs varied as a function of egg size and shell thickness and strength. Overall, domestic finch eggs provided a better alternative to quail eggs because they were small enough to allow detection of predation events by small mammals and did not have an unnatural odor like plasticine. Potential problems with nest concealment, egg visibility, egg odors, and other factors must be resolved to enhance the design and reliability of artificial nest experiments. *Received 21 September 1998, accepted 1 June 1999.*

COMPETITION FROM FOOD LIMITATION has been considered a key influence affecting the organization of avian communities (Martin 1987b). More recently, research has focused on nest predation as a process that determines community structure (e.g. Martin 1993a), particularly because predation is the primary cause of avian nesting mortality (Ricklefs 1969, Martin 1993a). Artificial nests have been widely used as a surrogate for natural nests to elucidate patterns of nest predation (e.g. Møller 1987, Gibbs 1991, Seitz and Zegers 1993), and, ultimately, to understand processes that shape life-history traits, habitat selection, and community patterns (Martin 1987a). Artificial nest studies have also been used to investigate causes of purported declines of North American songbirds (Rappole and McDonald 1994, Sauer et al. 1996) and to provide management recommendations for mitigating losses to predators (Wilcove 1985, Ammon and Stacey 1997). However, tests using artificial nests have been

relatively few in boreal forests, where deforestation and fragmentation are progressing at alarming rates, and high densities of breeding songbirds occur (Schieck et al. 1995, Kirk et al. 1996).

Artificial nests can facilitate controlled experiments with strong statistical designs (Reitsma et al. 1990), but these experiments often assume that predators search for and respond to artificial nests in the same way that they respond to natural nests (Martin 1987a). Some studies have found no difference in nesting success for artificial and natural nests (e.g. Gottfried and Thompson 1978, Andrén et al. 1985, Butler and Rotella 1998), whereas others have found success of artificial nests to be lower than natural nests (e.g. Ammon and Stacey 1997, Wilson et al. 1998) or vice versa (e.g. Roper 1992, Guyn and Clark 1997).

Predation of artificial nests may not be comparable to that of natural nests because of the appearance of artificial nests (Major and Kendal 1996). Conspicuousness of songbird nests varies with nest height and substrate (Martin 1993b, Howlett and Stutchbury 1996). Songbirds that build open-cup nests may minimize

[1] Address correspondence to this author at Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada. E-mail: sheila.rangen@ec.gc.ca

nest detection by predators by using materials that visually blend into the site surrounding a nest or that create a textured appearance (Harrison 1975). Unmodified wicker nests may be conspicuous (Reitsma et al. 1990, Gibbs 1991; but see Martin 1987a). Some experimenters dip nests in mud to modify their stark appearance (Cotterill 1996), but silhouettes of artificial nests nonetheless may be more distinct than those of natural nests.

Odors of humans, dummy eggs, and nest material may be present at artificial nests (Hoi and Winkler 1994, Whelan et al. 1994). In contrast, odors of adult birds and natural nests and eggs are absent (Møller 1987, Götmark 1992). Odors emanating from bird nests can either increase (Swennen 1968, Green and Anthony 1989) or decrease (Petit et al. 1989, Whelan et al. 1994, Clark and Wobeser 1997) clutch survival. Nocturnal mammals tend to respond more than birds to odors at natural and artificial ground nests (Storaas 1988, Bayne et al. 1997). Recent studies have used plasticine eggs to identify predators (Willebrand and Marcström 1988, Ammon and Stacey 1997, Hannon and Cotterill 1998), but the unnatural odor of plasticine may attract predators and inflate predation rates. Unusual odors due to egg age also may confound artificial nest studies (Major 1991), but this has rarely been tested (Henry 1969, Whelan et al. 1994).

Egg size and shell thickness may complicate the use of quail eggs (Roper 1992, DeGraaf and Maier 1996, Marini and Melo 1998). Predation by small mammals can be missed altogether when large quail eggs are used, leading to spurious conclusions for experimental treatments (Roper 1992, Bayne et al. 1997). Documenting predation events that would otherwise be missed by using quail eggs can be achieved by using plasticine eggs (Major et al. 1994, Bayne et al. 1997). However, eggs of domestic finches that are similar in size and strength to natural songbird eggs may result in more realistic predator responses than either quail or plasticine eggs, but to our knowledge this possibility has not been evaluated.

Using field and laboratory experiments, we investigated the response of predators to variation in artificial nest appearance and to the presence of quail, finch, and plasticine eggs. Because diurnal predators, particularly birds, rely heavily on visual cues (Howlett and Stutchbury 1996), we predicted that avian predators would find more wicker nests dipped in mud than wicker nests covered by a camouflage fabric. Because of the odor of plasticine eggs, artificial nests or egg assortments that contain plasticine eggs should suffer higher rates of predation when offered to deer mice (*Peromyscus maniculatus*) than nests or egg assortments that contain only finch and quail eggs. Mice and voles (hereafter, "mice") use olfaction to detect food and typically are unable to break quail eggs. Thus, we predicted that these predators would depredate a higher proportion of plasticine eggs than finch eggs and quail eggs, and a higher proportion of finch eggs than quail eggs, in field and laboratory experiments.

STUDY AREA AND METHODS

Study area.—Field sites were located in stands of boreal forest (14 to 60 ha) in west-central Alberta (elevation 1,060 to 1,170 m) that were logged from 1970 to 1972. The study area was highly fragmented by logging and oil and gas exploration, and stands were at least 60 km from the nearest human population (≥10,000 people). Within constraints of stand size, experimental plots were placed at least 50 m from stand edges that were often bordered by logging roads.

Stands were dominated by quaking aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*). White spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and balsam poplar (*Populus balsamifera*) comprised most of the remaining canopy. Understory was characterized, in decreasing importance, by willow (*Salix* spp.), green alder (*Alnus crispa*), bracted honeysuckle (*Lonicera involucrata*), cranberry (*Viburnum edule*), currant (*Ribes* spp.), and rose (*Rosa* spp.).

Potential mammalian predators in the study area included red squirrels (*Tamiasciurus hudsonicus*), northern flying squirrels (*Glaucomys sabrinus*), deer mice, red-backed voles (*Clethrionomys gapperi*), western jumping mice (*Zapus princeps*), least chipmunks (*Eutamias minimus*), alpine chipmunks (*Eutamias alpinus*), black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), pine martens (*Martes martes*), fishers (*Martes pennati*), least weasels (*Mustela nivalis*), long-tailed weasels (*Mustela frenata*), and short-tail weasels (*Mustela erminea*). Potential avian predators included Common Ravens (*Corvus corax*) and Gray Jays (*Perisoreus canadensis*).

Predator response to nest appearance.—We modified half of our commercial wicker nests (10 cm outside diameter, 6 cm deep) by sewing camouflage cloth to the outer surface and the rim of the nest bowl to break up the nest outline and to better mimic the ap-

pearance of natural nests. The pattern and colors of the material blended with the bark and foliage of trees in our area. We modified the remaining nests by dipping them in mud to reduce their brightness (hereafter, "mud" nests; Cotterill 1996). Nests were aired and lined with dry grass one week before use.

Five forest stands were selected, within which we established paired plots (1 ha) 100 m apart. Nest types (i.e. camouflage and mud) were randomly allocated to these paired plots. From 2 to 7 July 1996, we deployed 20 nests in each plot at random coordinates, using a 10 × 10 m grid scale, with the condition that nests were placed where songbirds would be expected to nest. Nests were randomly (yet evenly) distributed among five 1-m height classes ranging from 0.5 to 5.5 m. All nests were attached to substrates using monofilament line. We wore rubber gloves and boots during nest deployment and checks. One Japanese Quail (Coturnix japonica) egg and one plasticine egg, painted to resemble a quail egg, were placed in each nest. Nests were checked every five days over a 15-day period. A predation event was recorded if any egg was penetrated or missing, or if a plasticine egg contained tooth or bill marks. Penetrated eggs were classified as punctured, cracked, or broken.

Vegetation characteristics at nest sites were recorded at the end of the experiment. Plants were designated as trees or shrubs based on taxonomy. Measurements of large trees (>3 m tall) and large shrubs (≥1 m tall) were obtained using the point-quarter method (Krebs 1989). The area around each nest was divided into four equal quadrants, and distances to the nearest tree and green alder or willow were measured in each quadrant. Calculation of tree and shrub densities followed Krebs (1989), with the mean of the four distances equal to the square root of the mean area per plant. Plant species and height were identified and measured, respectively, for the nearest tree and shrub in each quadrant (trees ± 0.5 m; shrubs ± 0.1 m). Relative abundance of conifers versus deciduous trees and green alder versus willow were based on the frequency of species in the four quadrants. Small deciduous and coniferous trees (≤3 m) were counted in a 3-m radius around nests. Percent ground cover of bare ground and rock, ferns, grass/sedge, herbs, lichen, litter, moss, shrubs (<1 m), water, and woody debris was estimated visually in a 2-m radius surrounding nests. Heights of nest substrates were recorded. Horizontal and vertical concealment of nests were estimated visually 1 m from nests in the four cardinal directions as well as 1 m above and below nests. These estimates were averaged to obtain a single percentage value of a nest obscured by foliage. Tree and shrub closure was measured using a concave spherical densiometer (Lemmon 1956). Five observers collected vegetation data with observers measuring characteristics at an equal number of mud and camouflage nest sites. Vi-

sual estimations among investigators were calibrated prior to collecting these data.

Predator response to nest contents.—In each of eight forest stands, independent from the nest appearance experiment, nests were deployed (5 to 13 July 1997) at two locations (100 to 275 m apart), each containing three parallel transects (320 m long). Nests within stands were placed at least 800 m from those in replicate stands. At 40-m intervals along the three transect lines, single stations were erected across transects, totaling eight stations per location. Thus, each station contained three nests, one on each transect (25 m apart). Three egg treatments were randomly assigned to the three nest sites at each station, for a total of 384 nests (3 nests × 8 stations × 2 locations × 8 stands) and a density of 15 nests/ha. Pairing treatments at stations helped control for local vegetation effects. The rims of nest bowls were flush with the ground.

Wicker nests (9.5 cm outside diameter, 3.8 cm deep) were baited with (1) one quail egg and one finch egg; (2) one quail egg, one finch egg, and one plasticine egg; or (3) one quail egg, one finch egg, and five plasticine eggs. Each treatment contained 128 nests. Finch eggs were included in each nest to evaluate the importance of small rodents as egg predators. Quail and finch eggs were washed with tap water before use to remove odors and were visually inspected for cracks and punctures immediately before placement in nests. Finch eggs, obtained from hobby breeders in Canada and the United States, were refrigerated for up to two months before deployment in the field and were not refrigerated for less than seven days during transit to the study area. Finch eggs came from three species, but the color and size of the eggs were similar. Plasticine eggs simulated the size, shape, and color of white finch eggs and required no painting.

Predation rates on artificial nests were measured by examining loss of eggs from nests every four days during 12 days of exposure to predators. Nests containing only quail and finch eggs were considered destroyed by mice when (1) eggs were damaged and mouse scats were present at a nest; (2) finch eggs were damaged but quail eggs were intact; and (3) intact finch eggs had small incisor marks. All surviving finch eggs were opened at the end of the experiment to determine their state of deterioration. Concealment was measured at all nests as in the previous experiment.

Response of deer mice to plasticine eggs.—To confirm results of our field experiment, we offered wild deer mice assortments of eggs under controlled conditions. Mice were housed at room temperature and a natural photoperiod for at least 10 days prior to the experiment. Rodent chow was available *ad libitum* and was removed from cages 30 min before each trial. Forty mice (each used only once) were randomly given one of two egg assortments that had been used

in the field: (1) one finch egg and one quail egg; or (2) one finch egg, one quail egg, and one plasticine egg. We reasoned that the use of fresh finch eggs would eliminate any confounding effects that may have arisen from the use of old finch eggs in the field. Eggs were placed at random, 1 cm apart, in a row at the front of cages about 1 h after sunset. Mice were observed from behind a blind using an infrared lamp. The number of minutes to perform three foraging behaviors (touch with nose, bite, and penetrate) was recorded for all eggs. Time zero was recorded when mice approached eggs and subsequently touched at least one egg. Further contact with any egg could be interspersed with activities other than foraging (e.g. resting and grooming). From the time mice first approached eggs (and subsequently touched an egg), they were observed for 2.5 h.

Quail and finch eggshell measurements.—To obtain a relative index of the strength of finch and quail eggshells, eggs were depressed at the equator by a 2-mm probe that advanced at a constant rate of 0.2 mm/s with a 2-kg load cell using a food texture analyzer (Texture Technologies Corp. Model TA.XT2). The texture analyzer was set to penetrate to 3 mm after a sensory trigger force of 1 g was detected upon contacting the egg. The software package XT.RA dimension V3.5 (Stable Micro Systems, Surrey, England) recorded the force (kg) of depression on the egg when it fractured.

Length and breadth of all eggs were measured with Vernier calipers to the nearest 0.01 mm, and egg shape was determined by the ratio of length to breadth. Egg volume was calculated using the equation derived by Spaw and Rohwer (1987). Mean shell thickness (including membranes) was measured at three sites on egg equators with a micrometer (nearest 0.001 mm). Shells were oven dried at 50°C for 24 h prior to measurements.

Statistical analyses.—We used logistic regression to examine the effects of nest appearance and vegetation variables on nest fate. Two-way interactions with nest appearance were also investigated. To reduce multicollinearity, some vegetation variables that were highly correlated ($P \leq 0.01$) with other variables were deleted (e.g. retained variable = grass; deleted variables = litter, moss, woody debris). The most parsimonious model was attained by sequentially deleting nonsignificant interactions and then main effects. To determine if nests containing plasticine eggs were more susceptible to predation, we compared the mean number of days nests survived ($n = 8$ stands) among egg treatments using a Jonckheere (*J*) test for ordered alternatives (Siegel and Castellan 1988). This analysis tested the alternative hypothesis that the median number of days nests survived was ordered in magnitude for egg treatments: five plasticine/one quail/one finch < one plasticine/one quail/one finch < one quail/one finch. Pairwise comparisons followed Zar (1984). Logistic regression

was used to examine the relationship between concealment and fate as well as concealment and egg treatment. Statistical tests were conducted using SAS (1990).

RESULTS

Predator response to nest appearance.—Twenty-four percent of nests survived, 74% failed, and 2% were of unknown fate. Of depredated nests, 74% had both eggs destroyed and 26% had only one egg destroyed. Tooth and beak marks in plasticine eggs allowed predators to be identified at 49% of failed nests (birds 33%, squirrels 7%, small mammals 7%, mice 1%, large mammals 1%). A significant difference occurred in the number of plasticine eggs destroyed by birds and small mammals as a function of nest appearance ($G = 4.6$, df = 1, $P = 0.03$). This difference was caused by birds destroying more mud nests (29 of 36 destroyed) than camouflaged nests (20 of 35). Small mammals tended to depredate more camouflaged nests (15 of 35) than mud nests (7 of 36).

We used logistic regression to evaluate whether nest fate was related to nest appearance (mud vs. camouflage), nearest-neighbor distance, height class of nests, concealment, and vegetative characters ($n = 196$). When the model was reduced by eliminating nonsignificant interactions and then main effects (all $\chi^2 < 2.0$, all $P > 0.15$), the probability of a nest being depredated was not related to nest appearance ($\chi^2 = 0.0$, df = 1, $P = 0.96$). Increased cover by grass ($\chi^2 = 5.5$, df = 1, $P = 0.02$) and overall concealment by vegetation ($\chi^2 = 8.0$, df = 1, $P = 0.04$) enhanced nest survival, whereas more willow ($\chi^2 = 7.2$, df = 1, $P = 0.002$) and coniferous trees <3 m tall ($\chi^2 = 6.2$, df = 1, $P = 0.03$) at nest sites lowered nest survival. The biological relevance of vegetation variables in the model will be discussed elsewhere (Rangen et al. 2000).

Predator response to nest contents.—Predators of plasticine eggs visited 70.5% of deployed nests ($n = 384$). Mice destroyed the majority of plasticine eggs (59%), followed by unidentified predators (35%), small mammals (mice or squirrels; 3%), squirrels (2%), and large mammals (1%). The percentage of unidentified predators decreased two-fold when one plasticine egg was used and decreased an additional three-fold when five plasticine eggs were used. At nests visited by mice and unidentified

TABLE 1. Condition and number of finch and quail eggs in artificial nests visited by mice and unidentified predators in west-central Alberta, July 1997.

Predator	Finch eggs			Quail eggs		
	Intact	Penetrated	Missing	Intact	Penetrated	Missing
Mice	128	27	6	158	3	0
Unidentified	36	44	14	80	8	6

predators, 93.3% of the quail eggs remained intact (Fisher's exact test, $P = 0.001$; Table 1). In contrast, only 64% of the finch eggs remained intact ($G = 44.3$, df = 2, $P = 0.001$), and of those penetrated, 12% were cracked, 12% were broken, and 5% were punctured. Mice tended to leave finch eggs intact, whereas unidentified predators left similar numbers of intact and penetrated eggs (Table 1). At the end of the experiment, 62% ($n = 151$) of finch eggs appeared to be at some stage of decay, 26% ($n = 64$) were relatively fresh, and 12% ($n = 30$) were desiccated. Scats of mice were found at some nests of each treatment, but finch and quail eggs were not always penetrated. Mice were more likely to leave plasticine eggs in nests ($n = 134$) than remove one or more of them ($n \leq 11$; $G = 88.5$, df = 2, $P = 0.001$), whereas unidentified predators were more likely to remove eggs from nests than leave them (remaining = 16; one removed = 29; >one removed = 15; $G = 15.7$, df = 2, $P = 0.001$). Of nests containing plasticine eggs that were depredated by mice, 3% had no plasticine eggs, 71% had one plasticine egg, and 26% had more than one plasticine egg bitten ($G = 195.2$, df = 2, $P = 0.001$).

Contrary to results in the experiment on nest appearance, logistic regression indicated that nest failure was not related to concealment ($\chi^2 = 0.4$, df = 1, $P = 0.53$), and concealment did not vary with egg treatment ($\chi^2 = 1.2$, df = 2,

TABLE 2. Time taken by captive deer mice to touch, bite, and penetrate the first egg when presented with assortments of finch and quail eggs only versus assortments containing plasticine eggs. Values are $\bar{x} \pm$ SE in min, with n in parentheses.

Behavior	Finch and quail	Plasticine, finch, and quail	P[a]
Touch	0.9 ± 0.23 (19)	0.6 ± 0.15 (20)	0.22
Bite	10.6 ± 6.41 (19)	0.9 ± 0.21 (21)	0.03
Penetrate	40.3 ± 12.83 (12)	1.7 ± 0.44 (20)	0.002

[a] P-values from t-test.

$P = 0.55$). Predation rates were higher for nests that contained plasticine eggs versus quail eggs and finch eggs only (median survival = 10.2 days, $\bar{x} = 6.8 \pm$ SE of 0.8 nests destroyed, $n = 8$ stands), although not between nests containing one (median survival = 5.8 days, $\bar{x} = 13.1 \pm 1.0$ nests destroyed, $n = 8$ stands) versus five plasticine eggs (median survival = 5.4 days, $\bar{x} = 14.1 \pm 0.5$ nests destroyed, $n = 8$ stands; $J = 186$, $P = 0.005$). Similarly, the direction of the predicted order of predation was the same for all eight stands, with nests containing five plasticine eggs always having higher predation than nests containing one or no plasticine eggs, and nests containing one plasticine egg always having higher predation than nests containing no plasticine eggs. More finch eggs ($n = 111$) than quail eggs ($n = 42$) were penetrated (McNemar test, $\chi^2_c = 48.7$, $P = 0.001$), and more plasticine ($n = 196$) than finch eggs ($n = 61$) were penetrated ($\chi^2_c = 105.0$, $P = 0.001$) for treatments of one and five plasticine eggs combined (nests with five plasticine eggs only contributed one depredated plasticine egg to the sample size shown).

Response of captive deer mice to plasticine eggs.—Mice took 12 times longer to bite eggs in assortments of quail and finch eggs than in those that also contained plasticine eggs (Table 2). The time required to penetrate finch eggs in assortments of quail and finch eggs was 24 times longer than to penetrate eggs (finch or plasticine) in assortments that contained plasticine eggs. An overall effect of plasticine eggs occurred for two-egg assortments when all three foraging behaviors were analyzed (MANOVA, $F = 16.6$, df = 3 and 28, $P = 0.001$), but the tendency was weaker when touching and biting were evaluated alone ($F = 3.2$, df = 2 and 36, $P = 0.06$).

Within assortments of finch and quail eggs, more quail eggs ($n = 15$) than finch eggs ($n = 4$) were touched first ($\chi^2 = 6.4$, df = 1, $P = 0.01$), and overall, quail eggs were touched in less

TABLE 3. Time taken by captive deer mice to touch, bite, and penetrate a given egg type when presented with assortments of finch and quail eggs only versus assortments containing plasticine eggs. Values are medians in min, with range and n in parentheses.

| Behavior | Egg type | | | P |
	Plasticine	Finch	Quail	
		Finch and quail		
Touch	—[a]	0.7 (0.1 to 64.0, 19)	0.5 (0.1 to 3.8, 19)	0.001[b]
Bite	—	1.6 (0.4 to 110. 1, 17)	2.7 (0.2 to 132.4, 19)	0.001[b]
Penetrate	—	18.4 (3.2 to 129.6, 12)	—	—
		Plasticine, finch, and quail		
Touch	0.8 (0.1 to 7.9, 20)	0.8 (0.1 to 14.7, 20)	0.6 (0.2 to 103.9, 20)	0.890[c]
Bite	0.9 (0.1 to 8.0, 20)	1.3 (0.2 to 20.5, 19)	2.1 (0.3 to 103.9, 19)	0.160[c]
Penetrate	0.9 (0.1 to 7.9, 20)	4.7 (1.1 to 90.1, 14)	—	0.002[b]

[a] Dashes indicate that plasticine eggs were not part of finch and quail egg assortments, or no time to penetrate quail eggs was recorded.
[b] Wilcoxon signed-rank test.
[c] Kruskal-Wallis test.

time than were finch eggs (Table 3). However, finch eggs were bitten sooner ($\chi^2 = 12$, df $= 1$, $P = 0.001$) and had a greater number of eggs penetrated than did quail eggs (12 vs. 2).

Within assortments of plasticine eggs, finch eggs, and quail eggs, there was a weak tendency for more plasticine eggs ($n = 11$) than quail eggs ($n = 5$) or finch eggs ($n = 4$) to be bitten first ($\chi^2 = 4.3$, df $= 2$, $P = 0.12$). Nonetheless, more plasticine eggs were penetrated first ($\chi^2 = 16.2$, df $= 1$, $P = 0.001$), and plasticine eggs were penetrated in less time than finch eggs (Table 3). More plasticine eggs were punctured than the other two egg types (Cochran Q-tests, $Q = 24.6$, df $= 2$, $P = 0.001$), and more finch eggs than quail eggs were eaten ($Q = 57.4$, df $= 2$, $P = 0.001$). Plasticine eggs were touched, bitten, and penetrated all at once, whereas additional time was required for mice to penetrate finch eggs after touching them (Table 3).

Across assortments, most mice (93%, $n = 26$) broke into finch eggs at the small end of the egg, and no quail eggs were broken. From the time mice approached eggs, they had a mean of 9.4 ± 0.8 contacts ($n = 40$) with quail eggs, each contact lasting from 1 s to 5 min 46 s. Some mice were more aggressive in attempts to penetrate plasticine eggs and quail eggs when a food reward had already been received from a finch egg. Time spent during a single contact with quail eggs generally attenuated during a trial. Mice sometimes pressed quail eggs against their abdomen or the sides of the cage in attempts to open the eggs.

Egg measurements.—Quail eggs had larger

volumes ($\bar{x} = 8.78 \pm 0.14$ cm^3, $n = 52$) than finch eggs ($\bar{x} = 1.17 \pm 0.02$ cm^3, $n = 52$; $t = 52.7$, $P = 0.0001$). Quail eggshells were also 13 times stronger ($\bar{x} = 1.21 \pm 0.06$ kg, $n = 26$ vs. $\bar{x} = 0.09 \pm 0.004$ kg, $n = 26$; $t = 17.3$, $P = 0.0001$) and three times thicker ($\bar{x} = 0.25 \pm 0.003$ mm, $n = 52$ vs. $\bar{x} = 0.08 \pm 0.005$ mm, $n = 52$; $t = 30.7$, $P = 0.0001$) than finch eggs. Based on the ratio of length to breadth, finch eggs were more pyriform ($\bar{x} = 1.33 \pm 0.01$, $n = 52$) than quail eggs ($\bar{x} = 1.25 \pm 0.01$, $n = 52$; $t = -5.4$, $P = 0.0001$).

DISCUSSION

Many studies that use artificial nests have focused on the influence of habitat type, vegetation, spatial effects, nest density, and observer bias on nest predation (see Major and Kendal 1996). However, testing the reliability of experimental nests and egg types used in artificial nest studies is the first logical step required to improve our understanding of this experimental approach. Based on our results, simple modification of a wicker nest may not be adequate to simulate natural nests, but the choice of egg type appears to be critical in obtaining patterns of predation that more closely resemble natural situations.

Nest appearance.—Physical characteristics of artificial nests, including lining, size, and type, can influence predation (e.g. Møller 1987, Gibbs 1991). However, we found no evidence that avian predators perceived camouflaged and mud nests differently. Thus, both nest types may have been viewed merely as conspicuous,

dense objects. Cresswell (1997) claimed that predation of natural nests deployed in an artificial nest study was independent of physical traits of nests but was related to nest detectability and height. Nest visibility as it relates to concealment was important in explaining fate of our nests, and visibility often is reported to influence nesting success (e.g. Norment 1993, Gregg et al. 1994). It is possible that the lack of a nest-appearance effect was related to predators increasing their foraging rate to compensate for prey that was more difficult to find (i.e. a camouflaged nest; Guilford and Dawkins 1987, Lawrence 1989) or forming search images for eggs rather than nests (e.g. Vacca and Handel 1988, Hoi and Winkler 1994, Yahner and Mahan 1996).

The tendency of small mammals to preferentially depredate camouflaged nests may be similar to previous studies where predators preferentially depredated natural and wicker nests modified to simulate nests of specific species versus unmodified wicker nests (Martin 1987a, Gibbs 1991). It may be argued that such results support the "search-image" hypothesis (Martin 1987a) and that search images formed by predators for natural nests (or natural-looking artificial nests) are stronger than those formed for wicker nests. Because mammalian predators in our study do not rely solely on visual cues, attributes other than the appearance of wicker nests (e.g. dyes and chemicals in the camouflage fabric) may influence predation risk. Nonetheless, further tests of the search-image hypothesis require that predators be identified as visually or olfactorily oriented.

Predator response to egg type.—We demonstrated that different egg types measure different components of the predator assemblage, which explains some of the controversy in the literature. For example, higher predation rates have been documented for fragmented versus contiguous forest when only quail eggs were used (Wilcove 1985, Small and Hunter 1988, Burger et al. 1994). This may be due to a preponderance of avian predators at edges, typically corvids (Andrén 1992), that are capable of breaking quail eggs, but also to an inability to document predation by small mammals that prefer the forest interior (e.g. Wauters et al. 1994, Sekgororane and Dilworth 1995). Plasticine eggs, however, allow documentation of predation by these small mammals, resulting

in similar rates of predation for the two forest types (Nour et al. 1993), or higher predation in contiguous versus fragmented forests (Haskell 1995). Studies using plasticine eggs have reported higher predation rates for ground nests than for above-ground nests (Bayne et al. 1997), although patterns of predation for ground versus above-ground natural nests are inconsistent (Martin 1993b, Matsuoka et al. 1997). Plasticine eggs, therefore, may record predation events from small ground-dwelling mammals that are attracted to artificial nests and that otherwise would not visit natural nests.

Our field and laboratory experiments corroborated findings of other studies that mice were unable to break quail eggs (e.g. Roper 1992, Vander Haegen and DeGraaf 1996) and that quail eggs result in low predation (e.g. Nour et al. 1993, Bayne et al. 1997, Bayne and Hobson 1999). Quail eggs were simply too large for deer mice to grasp with their jaws, and the shells were stronger and thicker than those of songbirds and domestic finches (Spaw and Rohwer 1987, Picman et al. 1996). Some researchers have treated quail eggs with acetic acid to thin eggshells and then assumed that treated eggs can be penetrated by small mammals (Picman et al. 1993, Jobin and Picman 1997). Overall, if the species composition of small-gaped mammals is not the same among experimental treatments, quail eggs may not provide a reliable index of relative predation rates (Roper 1992, Haskell 1995). Nonetheless, quail eggs may be useful if larger species are the main predators in the community (Arango-Vélez and Kattan 1997, Craig 1998).

Mice rely strongly on their sense of smell while foraging (Howard et al. 1968, Anderson 1986). We found that predators, mostly mice, preferentially depredated nests that contained plasticine eggs, and we suspect that plasticine odors were responsible. Plasticine may result in higher rates of predation by attracting predators and by having a soft material that is easily penetrated compared with quail and finch eggs. If mammals that use olfactory cues comprise a large portion of the predator assemblage in one experimental treatment versus another (e.g. habitat type), differences in relative predation rates among experimental treatments may not be accurate. Predators preferred plasticine eggs even though finch eggs provided a food source; the same was observed with

captive deer mice. However, the number of plasticine eggs in nests did not influence the probability that eggs would be bitten. Once bitten, the taste of a plasticine egg, or the lack of a food reward, may have deterred small mammals from sampling other eggs. Results of another study suggested that mice were attracted to plasticine because mice were not primary predators of Song Sparrow (*Melospiza melodia*) nests until the nests were relocated and baited with quail eggs and plasticine eggs (Rogers et al. 1997). These results, however, could be an artifact of lack of parental activity at artificial nests (Verbeek 1970, Maxson and Oring 1978). Bayne and Hobson (1999) found that predators did not respond differently to quail eggs in artificial nests that had plasticine placed underneath versus nests that contained only quail eggs. Owing to the size and strength of quail eggs, however, Bayne and Hobson (1999) essentially were examining the response of squirrels rather than mice to plasticine odors.

Captive deer mice were attracted to egg assortments containing plasticine, supporting results of the artificial nest experiment and further suggesting that predators were not affected by the presence of old finch eggs (Whelan et al. 1994). If old finch eggs rather than plasticine had initially attracted mice to nests, this may have explained why only one plasticine egg was bitten instead of five, but it does not explain why mice did not eat old finch eggs.

The lower number of finch eggs versus plasticine eggs consumed in the wild may be related to egg condition for two reasons. First, small cracks and punctures in eggs may have provided sensory stimulation to animals sufficient to indicate that eggs were not highly palatable. However, cracked eggs can also increase the transmission of olfactory cues and increase predation (Olson and Rohwer 1998). Mice sometimes punctured eggs with their teeth at artificial nests, which also has been noted at natural nests (Maxson and Oring 1978). Thus, predation that destroys eggs but does not lead to their consumption may be typical in the wild. Second, handling times required by captive mice to break finch eggs were substantial (15 to 40 min). It is not known how much time and energy predators allocate to breaking eggs in the wild, but deer mice and red-backed voles spent no more than 15 s at artificial nests containing quail eggs in Minnesota (Fenske-Craw-

ford and Niemi 1997). Lack of a food reward seems an unlikely explanation for the short time mice spent at nests, because gray (*Sciurus carolinensis*) and red squirrels that can break quail eggs assessed nests for only 15 s and 42 s, respectively (Boag et al. 1984, Fenske-Crawford and Niemi 1997). Thus, foraging mice may investigate a potential food source, but if positive reinforcement is not obtained shortly thereafter, they may continue foraging elsewhere.

Conclusions.—Cues associated with artificial nests influenced rates of predation, emphasizing the need for investigators to match nest and egg models to predator assemblages. Given that small mammals may respond more naturally to artificial nests that closely simulate natural nests, exteriors of above-ground wicker nests should be modified with natural plant materials to imitate the nests of the bird species of interest.

Appropriate choices of egg types for artificial nest studies require knowledge of the composition of the predator assemblage. Composition of predator assemblages could be ascertained *a priori* by conducting point counts to census avian predators and diurnal squirrels, and by live trapping small nocturnal mammals, although the latter would be labor intensive. Alternatively, predator species composition could be assessed with various artificial nest experiments. First, "hair catchers" or cameras could be used in concert with finch eggs to identify predators with minimal interference from olfactory cues. Second, for each replicate plot of an experimental treatment, one-half of the randomly deployed nests could contain plasticine eggs and one-half could contain finch eggs (avoiding nearest-neighbor effects would be imperative). Third, a crossover experimental design would permit comparisons of predation rates using finch and plasticine eggs among and within replicate plots. Relative to natural eggs, plasticine eggs could allow twice as many predators to be identified. Nonetheless, we fully realize that any method of predator identification has inherent biases (Major 1991, Marini and Melo 1998).

Domestic finch eggs are likely the best alternative to wild songbird eggs for artificial nest studies because they capture predation events by all members of the predator assemblage, and they provide a natural food source that could

induce natural behavior from predators. If small mammals (diurnal or nocturnal) dominate the predator assemblage, then finch eggs rather than quail or plasticine eggs should be used to examine relative rates of predation. Either quail or finch eggs could be used for predator assemblages dominated by large mammals or birds. In conclusion, implications of using artificial nests must be fully understood if we wish to use these nests to test hypotheses under realistic conditions.

LITERATURE CITED

AMMON, E. M., AND P. B. STACEY. 1997. Avian nest success in relation to past grazing regimes in a montane riparian system. Condor 99:7–13.

ANDERSON, P. K. 1986. Foraging range in mice and voles: The role of risk. Canadian Journal of Zoology 64:2645–2653.

ANDRÉN, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. Ecology 73:794–804.

ANDRÉN, H., P. ANGELSTAM, E. LINDSTROM, AND P. WIDEN. 1985. Differences in predation pressure in relation to habitat fragmentation: An experiment. Oikos 45:273–277.

ARANGO-VÉLEZ, N., AND G. H. KATTAN. 1997. Effects of forest fragmentation on experimental nest predation in Andean cloud forest. Biological Conservation 81:137–143.

BAYNE, E. M., AND K. A. HOBSON. 1999. Do clay eggs attract predators to artificial nests? Journal of Field Ornithology 70:1–7.

BAYNE, E. M., K. A. HOBSON, AND P. FARGEY. 1997. Predation on artificial nests in relation to forest type: Contrasting the use of quail and plasticine eggs. Ecography 20:233–239.

BOAG, D. A., S. G. REEBS, AND M. A. SCHROEDER.

1984. Egg loss among Spruce Grouse inhabiting lodgepole pine forests. Canadian Journal of Zoology 62:1034–1037.

BURGER, L. D., L. W. BURGER, JR., AND J. FAABORG. 1994. Effects of prairie fragmentation on predation on artificial nests. Journal of Wildlife Management 58:249–254.

BUTLER, M. A., AND J. J. ROTELLA. 1998. Validity of using artificial nest to assess duck-nest success. Journal of Wildlife Management 62:163–171.

CLARK, R. G., AND B. K. WOBESER. 1997. Making sense of scents: Effects of odor on survival of simulated duck nests. Journal of Avian Biology 28:31–37.

COTTERILL, S. E. 1996. Effect of clearcutting on artificial egg predation in boreal mixedwood forests in north-central Alberta. M.S. thesis, University of Alberta, Edmonton.

CRAIG, D. P. 1998. Chipmunks use leverage to eat oversized eggs: Support for the use of quail eggs in artificial nest studies. Auk 115:486–489.

CRESSWELL, W. 1997. Nest predation: The relative effects of nest characteristics, clutch size and parental behavior. Animal Behaviour 53:93–103.

DEGRAAF, R. M., AND T. J. MAIER. 1996. Effect of egg size on predation by white-footed mice. Wilson Bulletin 108:535–539.

FENSKE-CRAWFORD, T. J., AND G. J. NIEMI. 1997. Predation of artificial ground nests at two types of edges in forest-dominated landscape. Condor 99:14–24.

GIBBS, J. P. 1991. Avian nest predation in tropical wet forest: An experimental study. Oikos 60:155–161.

GÖTMARK, F. 1992. The effects of investigator disturbance on nesting birds. Current Ornithology 9:63–104.

GOTTFRIED, B. M., AND C. F. THOMPSON. 1978. Experimental analysis of nest predation in an old-field habitat. Auk 95:304–312.

GREEN, G. A., AND R. G. ANTHONY. 1989. Nesting success and habitat relationships of Burrowing Owls in the Columbia basin, Oregon. Condor 91:347–354.

GREGG, M. A., J. A. CRAWFORD, M. S. DRUT, AND A. K. DELONG. 1994. Vegetational cover and predation of Sage Grouse nests in Oregon. Journal of Wildlife Management 58:162–166.

GUILFORD, T., AND M. S. DAWKINS. 1987. Search images not proven: A reappraisal of recent evidence. Animal Behaviour 35:1838–1845.

GUYN, K. L., AND R. G. CLARK. 1997. Cover characteristics and success of natural and artificial duck nests. Journal of Field Ornithology 68:33–41.

HANNON, S. J., AND S. E. COTTERILL. 1998. Nest predation in aspen woodlots in an agricultural area in Alberta: The enemy from within. Auk 115:16–25.

HARRISON, H. H. 1975. A field guide to birds' nests in the United States east of the Mississippi River. Houghton Mifflin, Boston.

HASKELL, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. Conservation Biology 9:1316–1318.

HENRY, V. G. 1969. Predation on dummy nests of ground-nesting birds in the southern Appalachians. Journal of Wildlife Management 33:169–172.

HOI, H., AND H. WINKLER. 1994. Predation on nests: A case of apparent competition. Oecologia 98: 436–440.

HOWARD, W. E., R. E. MARSH, AND R. E. COLE. 1968. Food detection by deer mice using olfactory rather than visual cues. Animal Behaviour 16: 13–17.

HOWLETT, J. S., AND B. J. STUTCHBURY. 1996. Nest concealment and predation in Hooded Warblers: Experimental removal of nest cover. Auk 113: 1–9.

JOBIN, B., AND J. PICMAN. 1997. Factors affecting predation on artificial nests in marshes. Journal of Wildlife Management 61:792–800.

KIRK, D. A., A. W. DIAMOND, K. A. HOBSON, AND A. R. SMITH. 1996. Breeding bird communities of western and northern Canadian boreal forest: Relationship to forest type. Canadian Journal of Zoology 74:1749–1770.

KREBS, C. J. 1989. Ecological methodology. Harper and Row, New York.

LAWRENCE, E. S. 1989. Why blackbirds overlook cryptic prey: Search rate or search image? Animal Behaviour 37:157–160.

LEMMON, P. E. 1956. A spherical densiometer for estimation of forest overstory density. Forest Science 2:314–320.

MAJOR, R. E. 1991. Identification of nest predators by photography, dummy eggs, and adhesive tape. Auk 108:190–195.

MAJOR, R. E., AND C. E. KENDAL. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: A review of methods and conclusions. Ibis 138:298–307.

MAJOR, R. E., G. H. PYKE, M. T. CHRISTY, G. GOWING, AND R. S. HILL. 1994. Can nest predation explain the timing of the breeding season and the pattern of nest dispersion of New Holland Honeyeaters? Oikos 69:364–372.

MARINI, M. Â., AND C. MELO. 1998. Predators of quail eggs, and the evidence of the remains: Implications for nest predation studies. Condor 100:395–399.

MARTIN, T. E. 1987a. Artificial nest experiments: Effects of nest appearance and type of predator. Condor 89:925–928.

MARTIN, T. E. 1987b. Food as a limit on breeding birds: A life-history perspective. Annual Review of Ecology and Systematics 18:453–487.

MARTIN, T. E. 1993a. Nest predation, nest sites, and birds: New perspectives on old patterns. BioScience 43:523–532.

MARTIN, T. E. 1993b. Nest predation among vegetation layers and habitat types: Revising the dogmas. American Naturalist 141:897–913.

MATSUOKA, S. M., C. M. HANDEL, AND D. D. ROBY. 1997. Nesting ecology of Townsend's Warblers in relation to habitat characteristics in mature boreal forest. Condor 99:271–281.

MAXSON, S. J., AND L. W. ORING. 1978. Mice as a source of egg loss among ground-nesting birds. Auk 95:582–584.

MØLLER, A. P. 1987. Egg predation as a selective factor for nest design: An experiment. Oikos 50:91–94.

NORMENT, C. J. 1993. Nest-site characteristics and nest predation in Harris' Sparrow and White-crowned Sparrows in the Northwest Territories, Canada. Auk 110:769–777.

NOUR, N., E. MATTHYSEN, AND A. A. DHONDT. 1993. Artificial nest predation and habitat fragmentation: Different trends in bird and mammal predators. Ecography 16:111–116.

OLSON, R., AND F. C. ROHWER. 1998. Effects of human disturbance on success of artificial duck nests. Journal of Wildlife Management 62:1142–1146.

PETIT, K. E., L. J. PETIT, AND D. R. PETIT. 1989. Fecal sac removal: Do the pattern and distance of dispersal affect the chance of nest predation? Condor 91:479–482.

PICMAN, J., M. L. MILKS, AND M. LEPTICH. 1993. Patterns of predation on passerine nests in marshes: Effects of water depth and distance from edge. Auk 110:89–94.

PICMAN, J., S. PRIBIL, AND A. K. PICMAN. 1996. The effect of intraspecific egg destruction on the strength of Marsh Wren eggs. Auk 113:599–607.

RANGEN, S. A., R. G. CLARK, AND K. A. HOBSON. 2000. Influence of nest site vegetation and predator community on the success of artificial songbird nests. Canadian Journal of Zoology 78: in press.

RAPPOLE, J. H., AND M. V. MCDONALD. 1994. Cause and effect in population declines of migratory birds. Auk 111:652–660.

REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus.* on nest predation in a northern hardwood forest: An artificial nest experiment. Oikos 57:375–380.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

ROGERS, C. M., M. J. TAITT, J. N. M. SMITH, AND G. JONGEJAN. 1997. Nest predation and cowbird parasitism create a demographic sink in wet-

land-breeding Song Sparrows. Condor 99:622–633.

ROPER, J. J. 1992. Nest predation experiments with quail eggs: Too much to swallow? Oikos 65:528–530.

SAS INSTITUTE. 1990. SAS/STAT user's guide, version 6, 4th ed. SAS Institute, Inc., Cary, North Carolina.

SAUER, J. R., G. W. PENDLETON, AND B. G. PETERJOHN. 1996. Evaluating causes of population change in North American insectivorous songbirds. Conservation Biology 10:465–478.

SCHIECK, J., M. NIETFELD, AND J. B. STELFOX. 1995. Differences in bird species richness and abundance among three successional stages of aspen dominated boreal forests. Canadian Journal of Zoology 73:1417–1431.

SEITZ, L. C., AND D. A. ZEGERS. 1993. An experimental study of nest predation in adjacent deciduous, coniferous and successional habitats. Condor 95:297–304.

SEKGORORANE, G. B., AND T. G. DILWORTH. 1995. Relative abundance, richness, and diversity of small mammals at induced forest edges. Canadian Journal of Zoology 73:1432–1437.

SIEGEL, S., AND N. J. CASTELLAN, Jr. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

SMALL, M. F., AND M. L. HUNTER. 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia 76:62–64.

SPAW, C. D., AND S. ROHWER. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. Condor 89:307–318.

STORAAS, T. 1988. A comparison of losses in artificial

and naturally occurring Capercaillie nests. Journal of Wildlife Management 52:123–126.

SWENNEN, C. 1968. Nest protection of eider ducks and shovelers by means of feces. Ardea 56:248–258.

VACCA, M. M., AND C. M HANDEL. 1988. Factors influencing predation associated with visits to artificial goose nests. Journal of Field Ornithology 59:215–223.

VANDER HAEGEN, W. M., AND R. M. DEGRAAF. 1996. Predation on artificial nests in forested riparian buffer strips. Journal of Wildlife Management 60:542–550.

VERBEEK, N. A. M. 1970. Breeding ecology of the Water Pipit. Auk 87:425–451.

WAUTERS, L., P. CASALE, AND A. A. DHONDT. 1994. Space use and dispersal of red squirrels in fragmented habitat. Oikos 69:140–146.

WHELAN, C. J., M. L. DILGER, D. ROBSON, N. HALLYN, AND S. DILGER. 1994. Effects of olfactory cues on artificial-nest experiments. Auk 111:945–952.

WILCOVE, D. D. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

WILLEBRAND, T., AND V. MARCSTRÖM. 1988. On the danger of using dummy nests to study predation. Auk 105:378–479.

WILSON, G. R., M. C. BRITTINGHAM, AND L. J. GOODRICH. 1998. How well do artificial nests estimate success of real nests? Condor 100:357–364.

YAHNER, R. H., AND C. G. MAHAN. 1996. Effects of egg type on depredation of artificial ground nests. Wilson Bulletin 108:129–136.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Engelwood Cliffs, New Jersey.

Associate Editor: B. A. Loiselle