

PREDATORS OF QUAIL EGGS, AND THE EVIDENCE OF THE REMAINS: IMPLICATIONS FOR NEST PREDATION STUDIES¹

MIGUEL Â. MARINI² AND CELINE MELO

Departamento de Biociências, Universidade Federal de Uberlândia, 38405-382, Uberlândia, Minas Gerais, Brazil

Abstract. We evaluated the consumption of Japanese Quail (*Coturnix coturnix*) eggs by captive reptiles, birds, and mammals in order to examine potential bias of nest predation experiments, and to determine whether predator identification through egg remains is reliable by the commonly used methods. Because none of the 86 individuals of 22 species of snakes consumed quail eggs in captivity, nest predation may be under-represented in artificial nest experiments. All three groups of predators left all types of egg remains, suggesting that researchers should refrain from classifying nest predators only by egg remains. The presence of scratches on quail eggs could be considered as a potential tool for reducing small-mouthed mammal bias on predation estimates in small-sized eggs in nest predation experiments.

Key words: artificial nests, egg remains, nest predation, predator behavior.

Artificial nest experiments using quail eggs are common (Wilcove 1985, Nour et al. 1993, Marini et al. 1995). Despite widespread use of this technique, it has biases (Willebrand and Marström 1988, Reitsma et al. 1990, Whelan et al. 1994) and the reliability of the results on estimates of relative nest predation levels have been questioned. Roper (1992), for example, showed that nest predation is underestimated because small mammals may be unable to handle large, thick-shelled quail eggs. Similarly, Nour et al. (1993) and Haskell (1995a, 1995b) questioned whether the conclusions of artificial nest predation experiments in fragmented forests reflect real trends in predation levels because eggs are being depredated only by part of the predator community. These criticisms, however, apply only when predation levels on quail eggs are compared with predation levels on smaller-sized bird eggs. Quail eggs may still be appropriate in estimating relative predation levels of similar-sized eggs. Larger eggs, such as those of Domestic Chicken, are appropriate in estimating predation levels of large-sized eggs, as was conducted by Andrén (1992) for woodland grouse. These criticisms may not apply for the

use of egg predation levels as an estimate of habitat use by predators (Andrén 1992).

Because of the importance of nest predation experiments in ecological theory (George 1987, Reitsma et al. 1990) and conservation studies (reviewed in Paton 1994), our objective is to examine whether this bias of nest predation experiments applies to a variety of predators. A complete understanding of the interactions between breeding birds and nest predators depends upon the identification of the predator species and of their relative impact on each nesting species. Attempts to identify nest predators are in general anecdotal and inconclusive. Usually most nest predators remain unidentified, or identified only as "mammals" or "birds." Our second objective is to determine whether predator identification through egg remains is reliable by the commonly used methods.

METHODS

We offered quail eggs (*Coturnix coturnix*) to reptiles (24 species, 105 individuals), birds (32 species, 132 individuals), and mammals (32 species, 198 individuals) kept in captivity at six zoological parks or serpentariums in Brazil. These animals were all healthy and known to eat regularly in captivity. Tests were conducted during September–October 1994, February–March and June 1995, and October–November 1996. We conducted tests with snakes only when the air temperature was above 20°C.

We offered one quail egg to each potential predator during its usual feeding time, but no other food. We assumed these animals were hungry because they normally were deprived of food for 24 hr (mammals and birds) or for 7–10 days (reptiles). Each animal was observed for up to 1 hr or until it showed a response to the egg. For each trial, we recorded whether it ate the egg, the condition of the shell remains (intact, with holes, partially destroyed, totally destroyed, fragmented, or swallowed whole) and of the egg contents (totally consumed, partially consumed, or not consumed). For snakes, we conducted two sets of tests. First, we offered eggs at air temperature. Then, at least one month after the test with air-temperature eggs, 17 individuals (Table 1) were offered eggs pre-heated for 1 hr to 37–38°C (mean incubation temperature of birds; Gill 1990).

RESULTS

None of the 86 individuals of 22 species of snakes showed any response to the room temperature eggs offered, nor did the 17 individuals of 9 species offered

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² Current address: Departamento de Biologia Geral, ICB, C.P. 486, Universidade Federal de Minas Gerais, 30161-970, Belo Horizonte, MG, Brazil, e-mail: marini@mono.icb.ufmg.br

TABLE 1. Species of reptiles, birds, and mammals offered quail eggs in captivity and their pattern of consumption.

Species	Common names	Natural diets ^a	Eat eggs?	Type of shell remain ^b
Reptilia (24 species, 105 individuals)		C, O	Y, N	I, S
Ophidia ^c		C	N	I
Lacertilia		O	Y	S
<i>Tupinambis meriane</i> (9) ^d	Teju	O	Y	S
<i>Iguana iguana</i> (10)	Iguana	O	Y	S
Aves (32 species, 132 individuals)		C, F, G, H, I, O, R	Y, N	F, H, I, P, S, T
Tinamidae		G, O	Y, N	H, I, P
<i>Crypturellus undulatus</i> (1)	Undulated Tinamou	G	N	I
<i>Crypturellus parvirostris</i> (1)	Small-billed Tinamou	G	N	I
<i>Rhynchotus rufescens</i> (12)	Red-winged Tinamou	O	Y	H, I, P
Ciconiiformes		C	N	I
<i>Harpipion caerulescens</i> (3)	Plumbeous Ibis	C	N	I
<i>Theristicus caudatus</i> (8)	Buff-necked Ibis	C	N	I
Falconiformes		C, R	Y, N	H, I, P, T
<i>Caracara plancus</i> (8)	Crested Caracara	C	Y	H, I, P, T
<i>Milvago chimachima</i> (6)	Yellow-headed Caracara	C	Y	H
<i>Buteo magnirostris</i> (4)	Roadside Hawk	C	N	I
<i>Buteo albicaudatus</i> (1)	White-tailed Hawk	C	N	I
<i>Falco sparverius</i> (5)	American Kestrel	C	N	H, I
<i>Sarcorrhampus papa</i> (6)	King Vulture	R	Y	I, P, T
<i>Geranoaetus melanoleucus</i> (2)	Black-chested Buzzard-eagle	C	N	I
Galliformes		O	Y, N	H, I, P, T
<i>Penelope ochrogaster</i> (1)	Chestnut-bellied Guan	O	Y	H
<i>Penelope supercilialis</i> (3)	Rusty-margined Guan	O	N	I
<i>Penelope jacucaca</i> (3)	White-browed Guan	O	N	H
<i>Crax fasciolata</i> (11)	Bare-faced Curassow	O	Y	H, I, P, T
<i>Mitu mitu</i> (5)	Razor-billed Curassow	O	Y	T
Gruiformes		O	Y	F, H, I, P, S, T
<i>Aramides cajanea</i> (7)	Gray-necked Wood-rail	O	Y	F, H, I, P
<i>Cariama cristata</i> (10)	Red-legged Seriema	O	Y	F, H, I, P, S, T
Piciformes		O	Y, N	H, I, P, S, T
<i>Ramphastos toco</i> (14)	Toco Toucan	O	Y	H, I, P, S, T
<i>Ramphastos dicolorus</i> (4)	Red-breasted Toucan	O	N	I, P
Passeriformes		F, G, O	Y, N	H, I, P
<i>Cyanocorax cristatellus</i> (3)	Curl-crested Jay	O	Y	H, P
<i>Cyanocorax chrysops</i> (2)	Plush-crested Jay	O	Y	H
<i>Cyanocorax caeruleus</i> (3)	Azure Jay	O	Y	H, I
<i>Turdus rufiventris</i> (1)	Rufous-bellied Thrush	O	N	I
<i>Piranga flava</i> (1)	Hepatic Tanager	F	N	I
<i>Ramphocelus bresilius</i> (1)	Brazilian Tanager	F	N	I
<i>Cissopis leveriana</i> (1)	Magpie Tanager	F	N	I
<i>Paroaria dominicana</i> (2)	Red-cowled Cardinal	G	N	I
<i>Paroaria coronata</i> (1)	Red-crested Cardinal	G	N	I
<i>Gnorimopsar chopi</i> (1)	Chopi Blackbird	G	N	I
<i>Molothrus bonariensis</i> (1)	Shiny Cowbird	G	N	I
Mammalia (32 species, 199 individuals)		C, F, G, H, I, O, R	Y, N	F, H, I, P, S, T

TABLE 1. Continued.

Species	Common names	Natural diets ^a	Eat eggs?	Type of shell remain ^b
Primates				
<i>Callithrix geoffroyi</i> (2)	Geoffroy's tufted-ear marmoset	F, G, H, I, O	Y, N	F, H, I, P, T
<i>Callithrix penicillata</i> (6)	Black ear-tufted marmoset	G, O	N	I
<i>Leontopithecus chrysomelas</i> (3)	Golden-headed lion tamarin	I, O	Y	H, I, P
<i>Leontopithecus rosalia</i> (2)	Golden lion tamarin	I, O	N	I
<i>Leontopithecus chrysopygus</i> (2)	Black lion tamarin	I, O	N	I
<i>Alouatta caraya</i> (4)	Howling monkey	F, H	Y	F, P
<i>Alouatta fusca</i> (1)	Brown howling monkey	F, H	Y	T
<i>Aotus trivirgatus</i> (3)	Night monkey	F, O	Y	H, I, P
<i>Ateles paniscus</i> (6)	Spider monkey	F, H	Y	F, H
<i>Cebus apella</i> (11)	Tufted capuchin	F, O	Y	F, P, T
<i>Saimiri sciureus</i> (4)	Squirrel monkey	F, O	Y	T
Carnivora				
<i>Cerdocyon thous</i> (4)	Crab-eating fox	C, F, I, O	Y, N	F, H, I, P, S, T
<i>Chrysocyon brachyurus</i> (11)	Maned wolf	I, O	Y	F
<i>Lycalopex vetulus</i> (13)	Hoary fox	I, O	Y	F, I, P, T
<i>Nasua nasua</i> (17)	Coatimundi	F, O	Y	F, P, T
<i>Procyon cancrivorus</i> (11)	Crab-eating raccoon	F, O	Y	F, T
<i>Eira barbara</i> (10)	Tayra	C	Y	I, P, T
<i>Galictis vittata</i> (1)	Greater grison	C	e	e
<i>Felis catus</i> (3)	Domestic cat	C	N	I
<i>Herpailurus yagouaroundi</i> (5)	Yagouaroundi	C	N	I
<i>Leopardus pardalis</i> (15)	Ocelot	C	Y	F, H, I, P
<i>Leopardus tigrinus</i> (4)	Little spotted cat	C	N	I
<i>Panthera onca</i> (3)	Jaguar	C	Y	I, S
<i>Puma concolor</i> (4)	Cougar	C	Y	I, T
Artiodactyla				
<i>Pecari tacaju</i> (6)	Collared pecary	F, H	Y, N	I
<i>Tayassu pecari</i> (4)	White-lipped pecary	F, H	N	I
Rodentia				
<i>Mus musculus</i> (6)	House mouse	F, O	Y, N	I, H, P, T
<i>Rattus rattus</i> (20)	Roof rat	O	N	I
<i>Calomys callosus</i> (6)	New World mouse	O	Y	H, I, P, T
<i>Coendou prehensilis</i> (4)	Prehensile-tailed porcupine	F, G	N	I
<i>Sphiggurus villosus</i> (3)	Long-spined porcupine	F, G	N	I
<i>Agouti paca</i> (5)	Agouti	F	Y	F, T

^a C = Carnivore; F = Frugivore; G = Granivore; H = Herbivore; I = Insectivore; O = Omnivore; R = Carrion.

^b F = Fragmented (small shell fragments); H = Hole; I = Intact; P = Partially destroyed (half shell); S = Swallowed the egg whole; T = Totally destroyed (shell crushed but not fragmented).

^c Species (number of individuals offered air-temperature, and pre-heated eggs, respectively) of snakes that did not consume eggs included: *Boa constrictor* (10, 2), *Eunectes murinus* (5), *Epicrates cenchria* (9, 2), *Corallus enhydris* (1), *Philodryas olfersii* (2, 2), *Philodryas naterreri* (2), *Pseudoboa nigra* (1), *Spilotes pulatus* (5), *Oxyrhopus trigeminus* (3), *Oxyrhopus rombifer* (1), *Liophis almadensis* (2), *Helicop carinicaudus* (1), *Drymarchon corais* (1), *Micrurus frontalis* (2, 2), *Masticodyras bifasciatus* (3), *Bothrops itapetininge* (3), *Bothrops alternatus* (3, 2), *Bothrops moogeni* (11, 2), *Bothrops neuwied* (6, 2), *Crotalus durissus* (12, 2), *Clelia clelia* (1), *Waglerophis merremii* (2, 1).

^d Number in parentheses represents number of individuals tested.

^e Carried the egg to the den.

heated eggs (Table 1). Among reptiles, only lizards, tejus *Tupinambis meriane*, and iguanas *Iguana iguana*, depredated all the eggs offered by swallowing them whole.

Among birds, 13 (40.6%) species consumed eggs (Table 1). Frugivore and granivore birds did not eat the eggs, but most (71.4%) omnivore birds did. Among mammals, 19 species (61.3%; the greater grison, *Galictis vittata*, excluded) consumed the eggs (Table 1). There was no clear relationship between mammalian diet and egg-eating, because species from all dietary groups consumed eggs. Among the three small-mouthed rodents tested (house mouse, *Mus musculus*;

New World mouse, *Calomys callosus*; and roof rat, *Rattus rattus*), only the larger roof rat was able to consume the eggs, reinforcing Roper's (1992) and Haskell's (1995b) findings.

Egg-eating by both birds and mammals produced all kinds of egg remains (Table 1). Birds may leave no traces of egg shells (Toco Toucan, *Ramphastos toco*; and the Red-legged Seriema, *Cariama cristata*), leave shell fragments of variable sizes (Bare-faced Curassow, *Crax fasciolata*; and the Crested Caracara, *Caracara plancus*), or mainly holes (jays, *Cyanocorax* spp.). The same species, however, may leave different types of shell re-

mains (Gray-necked Wood-rail, *Aramides cajanea*; the Crested Caracara, and the Toco Toucan) (Table 1). When birds were able to break the shell, they usually ate the egg contents. Birds, in general, hit the egg against a substrate, damaging the shell considerably.

Mammals, like birds, left all kinds of shell fragments after consuming the egg (Table 1). In general, they damaged the shell, which could be eaten or not, and ate the egg contents. The roof rat had the most variable egg consumption (but also the species with most individuals tested, $n = 20$), leaving all kinds of egg remains, including holes.

Egg consumption and handling varied considerably among animals. Falconiforms, in general, consumed the egg where they found it. The Crested Caracara held the egg with the foot and punctured it with the beak before eating. The Bare-faced and the Razor-billed Curassow (*Mitu mitu*) punctured the egg where they found it and ate the leaked contents from the ground. The Gray-necked Wood-rail carried the egg to a small pond and washed it several times before puncturing and eating it. Both toucans carried the egg to a perch before consuming it. Among the passeriforms, the Azure Jay (*Cyanocorax caeruleus*) carried the egg away, hid it among rocks or tree forks, and later returned to it to eat. The Curl-crested Jay (*Cyanocorax cristatellus*) first punctured and abandoned the egg where it was found, then hid the broken shells under rocks. Some passeriforms (Rufous-bellied Thrush, *Turdus rufiventris*; Red-cowled Cardinal, *Paroaria dominicana*; Red-crested Cardinal, *P. coronata*; and the Shiny Cowbird, *Molothrus bonariensis*) tried to puncture the egg without succeeding.

Mammals utilized either a substrate, canine teeth, or their claws to puncture the shells (some monkeys; the tayra, *Eira barbara*; and the coatimundi, *Nasua nasua*). The hoary fox (*Lycalopex vetulus*) was the only mammal to use the snout to break the shell, which did not cause much damage to the egg shell. Monkeys usually carried the egg away. Tufted capuchins (*Cebus apella*) used the canines, claws, and even pointed tips of the cage fence to puncture the egg before eating all the egg content and the shell, leaving only small fragments. The greater grison carried the egg to its den, where it may have consumed the egg. The two smallest rodents (house mouse and New World mouse) tried to break the egg shell, but did not succeed. Some mice, however, rolled the egg on the ground and hid it under the cage dirt.

DISCUSSION

These data suggest that if snakes behave in the field as they behaved in captivity, field estimates of nest predation levels using artificial nests may not evaluate the impact of snakes on nesting bird communities. Our results are in agreement with the fact that no study has ever recorded snakes depredating an egg in an artificial nest, although snakes may attack natural nests (Best 1974) and drive bird species to extinction by depredating their nests (Savidge 1987). Even photographic camera studies (Reitsma et al. 1990, Leimgruber et al. 1994), one of the most efficient methods of identifying nest predators, have never reported snakes depredating artificial nests. The relative impact of snakes on bird nesting communities is poorly known. In some cases,

such as in North American prairies (Best 1978) and islands (Savidge 1987), snakes are among the most important nest predators. George (1987) suggested that mammals and snakes have a significant impact as predators of artificial nests, and snakes have been deemed responsible for the depredation of above-ground nests in Panama (Loiselle and Hoppes 1983). Skutch (1985) also suggested that snakes are major nest predators in the tropics. Cadle and Greene (1993) list birds and bird eggs in the diet of 12 genera of colubrine snakes (Colubridae), and consider eggs frequent in the diet of *Oxybelis* and *Pseustes* species. Here, we tested 15 individuals of five snake genera (*Philodryas*, *Pseudoboa*, *Spilotes*, *Liophis*, and *Mastigodryas*) known to have birds and/or eggs in their diet. The underestimate of artificial nest predation levels caused by the lack of nest predation by snakes should be evaluated further on a habitat by habitat basis.

Best (1978) developed criteria for distinguishing predators of natural nests and identified as nest predators: (a) snakes, when the nest or surrounding vegetation were undisturbed, or the nest had a circular hole in the bottom, (b) larger mammals when the nest was tilted, or partially or entirely torn, with the surrounding vegetation matted down to a varying extent, and (c) smaller mammals when there was partial removal of the nest contents, presence of egg shell fragments in the nest vicinity, and small disturbance to the nest. However, little or no evidence of nest disturbance, can be misleading evidence of the type of nest predator because different types of predators (Franklin's ground squirrel, *Spermophilus franklinii*, Sowls 1948; Gray Jay, *Perisoreus canadensis*, Ouellet 1970; and snakes, Best 1974, Skutch 1985) may leave no evidence after depredating nests. In contradiction to Best (1978), others (Skutch 1985, Vacca and Handel 1988) considered that nests with egg fragments found in or near the nest were depredated by birds, and nests with no traces of eggshells were depredated by mammals. Skutch (1985) stated that mammalian predators often leave shell fragments in the nest.

Holes in the eggs have been assumed to be produced only by birds. However, several mammals tested by us produced holes in the eggs, namely the roof rat, the ocelot (*Leopardus pardalis*), the maned wolf (*Chrysocyon brachyurus*), the night monkey (*Aotus trivirgatus*), the spider monkey (*Ateles paniscus*), and the black ear-tufted marmoset (*Callithrix penicillata*). A single species of predator may treat bird eggs in various ways. For example, red squirrels (*Tamiasciurus hudsonicus*) treated quail eggs by puncturing and leaving the egg *in situ*, making a large hole, or carrying the egg away (Boag et al. 1984).

Rats and mice left abundant claw and tooth marks on unbroken egg shells. This fact may enable one to evaluate small rodent nest predation by considering scratched eggs as depredated. This finding may improve artificial nest experiment methodology because the bias of no nest depredation by small-mouthed mammals could be reduced. One can assume that had these small-mouthed mammals encountered a small, thin-shelled bird egg instead of a quail egg, it would have been depredated.

Egg remains are not good indicators of the type of

nest predator. Egg remains in our study suggest that they cannot be ascribed with certainty to either birds or mammals. We suggest that future studies utilizing quail eggs as bait in artificial nests consider two predation estimates. First, consider scratched eggs as depredated (as has been done by Langen et al. 1991) for estimates of depredation of both similar- and smaller-sized eggs. However, eggs must be checked for scratches before placing them in the field because some eggs already have scratches. Second, if scratched eggs are not considered as depredated, then estimates of nest predation based upon such eggs should be calculated only relative to similar-sized eggs.

Our data enable us to raise three points: (1) snake nest predation may be under-represented in artificial nest experiments with quail eggs, (2) researchers should refrain from classifying nest predators only by egg remains, and (3) the presence of scratches on quail eggs could be considered as a potential tool for reducing small-mouthed mammal bias on predation estimates of small-sized eggs. Artificial nest experiments abound in the ecological and conservation literature, and criticisms and improvement of this methodology are desirable.

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LITERATURE CITED

- ANDRÉN, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73:794–804.
- BEST, L. B. 1974. Blue racers prey on Field Sparrow nests. *Auk* 91:168–169.
- BEST, L. B. 1978. Field Sparrow reproductive success and nesting ecology. *Auk* 95:9–22.
- BOAG, D. A., S. G. REEBS, AND M. A. SCHROEDER. 1984. Egg loss among Spruce Grouse inhabiting lodgepole pine forests. *Can. J. Zool.* 62:1034–1037.
- CADLE, J. E., AND H. W. GREENE. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages, p. 281–293. *In* R. E. Ricklefs and D. Schluter [eds.], *Species diversity in ecological communities*. Univ. Chicago Press, Chicago.
- GEORGE, T. L. 1987. Greater land bird densities on island vs. mainland: relation to nest predation level. *Ecology* 68:1393–1400.
- GILL, F. B. 1990. *Ornithology*. W. H. Freeman, New York.
- HASKELL, D. G. 1995a. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conserv. Biol.* 9:1316–1318.
- HASKELL, D. G. 1995b. Forest fragmentation and nest-predation: are experiments with Japanese Quail eggs misleading? *Auk* 112:767–770.
- LANGEN, T. A., D. T. BOLGER, AND T. J. CASE. 1991. Predation on artificial bird nests in chaparral fragments. *Oecologia* 86:395–401.
- LOISELLE, B. A., AND W. G. HOPPE. 1983. Nest predation in insular and mainland lowland rainforest in Panama. *Condor* 85:93–95.
- LEIMGRUBER, P., W. J. MCSHEA, AND J. H. RAPPOLE. 1994. Predation on artificial nests in large forest blocks. *J. Wildl. Manage.* 58:254–260.
- MARINI, M. A., S. K. ROBINSON, AND E. J. HESKE. 1995. Edge effects on nest predation in the Shawnee National Forest, southern Illinois. *Biol. Conserv.* 74:203–213.
- 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.
- OUELLET, H. 1970. Further observations on the food and predatory habits of the Gray Jay. *Can. J. Zool.* 48:327–330.
- PATON, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conserv. Biol.* 8:17–26.
- REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunk, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57:375–380.
- ROPER, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? *Oikos* 65:528–530.
- SAVIDGE, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68:660–668.
- SKUTCH, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithol. Monogr.* 36:575–594.
- SOWLS, L. K. 1948. The Franklin ground squirrel *Citellus franklinii* (Sabine) and its relationship to nesting ducks. *J. Mammal.* 29:113–137.
- VACCA, M. M., AND C. M. HANDEL. 1988. Factors influencing predation associated with visits to artificial goose nests. *J. Field Ornithol.* 59:215–223.
- 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. S. 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 artificial nests to study predation. *Auk* 105:378–379.