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ABSTRACT

Little information exists that can be used to accurately identify predator species responsible for destruction of northern bobwhite (*Colinus virginianus*) nests. We used remotely-tripped cameras to photograph nest predators at 25 wild bobwhite nests that were continually filled with eggs from pen-raised quail. Data describing depredation events were collected to characterize species-specific damage patterns. Seven species of nest predators were photographed 1,797 times from June to October 1996. We describe depredation patterns for opossums (*Didelphis marsupialis*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), and domestic dogs (*Canis familiaris*). These descriptions should help researchers identify the predator species responsible for destroyed bobwhite nests.

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INTRODUCTION

Nest depredation is the primary cause of northern bobwhite nest failure throughout their range (Stoddard 1931, Rosene 1969, Klimstra and Roseberry 1975, Simpson 1976, Lehman 1984, DeVos and Mueller 1993, Burger et al. 1995, Puckett et al. 1995, Hurst et al. 1996). Unfortunately, little information exists that provides an objective basis for accurately determining which predator species are responsible for specific depredation events. Most published reports providing diagnostic information for interpreting evidence at destroyed nests are based on studies of waterfowl (Reardon 1951) or other species (Darrow 1938, Mosby and Handley 1943, Einarsen 1956). The criteria used to describe such evidence are often ambiguous and sometimes contradictory (Baker 1978, Sargeant et al. 1998). As a result, estimates of the proportion of nests destroyed by individual predator species are frequently based on conjecture, and are therefore potentially inaccurate.

Although researchers have long recognized the need for accurately characterizing species-specific nest depredation patterns, few objective techniques have been available to address the problem. Studies attempting to distinguish patterns of predation have utilized captive-fed animals (Stoddard 1931, Darrow 1938), hair catchers (Baker 1980, Trevor et al. 1991), animal tracks (Nelson and Handley 1938, Reardon 1951), and direct field observations (Einarsen 1956). These techniques are often impractical or involve subjective assessments that make accurate diagnoses difficult, especially in complex predator communities. The recent use of remotely-tripped cameras has enabled investigators to photograph nest predators at simulated ("dummy") nests (Martin et al. 1987, Picman 1987, Leimgruber et al. 1994, Picman and Schriml 1994) and to link evidence at depredated nests to the responsible predator species (Hernandez et al. 1997). In this study, we used remotely-tripped cameras to identify nest predators and then quantify physical evidence at the depredated nest. The information presented in this paper should be useful to researchers attempting to assess which predator species are responsible for destroyed bobwhite nests.

METHODS

We conducted our study on 13 privately owned farms in Amelia County, located in south-central Virginia, from June to October 1996. Camera units triggered by passive infrared sensors (Cam Trakker®) were installed at 25 nests that had previously been incubated by wild, radio-tagged bobwhites. All nests had either hatched ($n = 4$) or been depredated ($n = 21$) prior to camera installation. Camouflaged camera units were mounted on metal stakes approximately 2 to 3 meters from the nest and 1 meter above the ground. The passive infrared beam was aligned to trigger the camera to photograph any animals approaching within 0.25 meters of the nest. Cameras contained an automatic film advance and were programmed for a 3-minute time delay between photographs. Cameras were operational 24 hours per day and equipped with an automatic flash for night photography. Each photograph was imprinted with the date and time that the event occurred.

Twelve eggs from pen-raised bobwhites were

placed into each nest, closely approximating the average size clutch for wild bobwhites in Virginia (Fies, unpublished data). A bobwhite wing was placed over the clutch to conceal the eggs and simulate the presence of an incubating bird. All nests were monitored daily, usually during morning hours, and replenished with fresh eggs after each depredation event.

Physical evidence at depredated nests was quantified using procedures described by Sargeant et al. (1998). The number, extent of damage, and spatial arrangement of eggshell remains were documented on data sheets and photographed with a Polaroid® camera. Additional evidence (tracks, feces, etc.) was noted when present. All eggshell remains were collected, labeled, and stored in a freezer for verification purposes.

Slides taken by remote camera units were catalogued and examined for the presence of nest predators. Incidental observations of other species were also noted. At each nest, the number of different individuals of each species photographed was estimated by comparing pelage markings. Only data from depredation events involving a single species of nest predator were used to characterize damage patterns. Events involving multiple species of predators, or where the camera ran out of film during the depredation event, were excluded from analyses. Average values for depredation variables were calculated using Microsoft Access®, version 2.0.

RESULTS

Twenty-two different animal species were photographed 1,966 times at 25 nests (Table 1). Seven species (n = 1,797 photographs) were observed depredating eggs and 15 species were photographed at nests that were undisturbed or had previously been destroyed. Striped skunks and opossums were the species most frequently photographed, accounting for 41.4% and 36.5% of the nest predator photographs, respectively. Other species photographed destroying nests, in order of frequency, included the domestic dog (9.0%), gray fox (8.1%), raccoon (4.0%), groundhog (*Marmota monax*) (0.6%), and black rat snake (*Elaphe obsoleta obsoleta*) (0.4%). Species photographed, but not confirmed as nest predators, included the hispid cotton rat (*Sigmodon hispidus*), white-footed mouse (*Peromyscus leucopus*), domestic cat (*Felis catus*), and bobcat (*Lynx rufus*). Incidental photographs were taken of whitetail deer (*Odocoileus virginianus*), domestic cattle (*Bos taurus*), eastern cottontails (*Sylvilagus floridanus*), an eastern gray squirrel (*Sciurus carolinensis*), and an eastern chipmunk (*Tamius striatus*). Bird species photographed included northern bobwhite, mourning dove (*Zenaida macroura*), northern mockingbird (*Mimus polyglottos*), brown thrasher (*Toxostoma rufum*), and brown-headed cowbird (*Molothrus ater*).

Single-species depredation data were obtained for 222 events involving at least 44 individuals of 5 nest predator species. The amount of eggshell evidence, extent of eggshell damage, and arrangement of eggshells at depredated nests varied between species (Table 2).

Table 1. Minimum number of individual animals and the number of times species were photographed (% in parentheses) with remotely-tripped cameras at artificial bobwhite nests (n = 25) in Virginia, June–October 1996.

	Minimum number of individuals	Number of photographs
Actual nest predators		
skunk	15	744 (41.4)
opossum	20	655 (36.5)
dog	17	162 (9.0)
gray fox	4	146 (8.1)
raccoon	16	71 (4.0)
groundhog	3	11 (0.6)
black rat snake	4	8 (0.4)
Total	79	1,797 (100.0)
Potential nest predators/shell scavengers		
cotton rat	1	85 (66.9)
white-footed mouse	3	35 (27.6)
domestic cat	3	5 (3.9)
bobcat	2	2 (1.6)
Total	9	127 (100.0)
Other species		
northern bobwhite	2	12 (28.6)
mockingbird	2	10 (23.8)
unknown bird species	5	5 (11.9)
cow	2	3 (7.1)
brown thrasher	1	2 (4.8)
mourning dove	1	2 (4.8)
whitetail deer	2	2 (4.8)
eastern cottontail	2	2 (4.8)
eastern gray squirrel	1	2 (4.8)
eastern chipmunk	1	1 (2.3)
brown-headed cowbird	1	1 (2.3)
Total	20	42 (100.0)
All species	108	1,966

Opossum

Nest depredation data were collected for 15 opossums that destroyed 110 nests. Opossums usually ate most of the eggs in the clutch ($\bar{x}$ = 9.6), but left 1 or more whole eggs in many (50.0%) of the depredated nests. Opossums removed eggs from the nest with their mouth, but usually held them between their front paws to consume them. After biting into the shell to expose the yolk, the entire egg was placed into the mouth and chewed up. The chewed shell was swallowed entirely or spit out.

Eggshell evidence was present at 96 of 110 (87.3%) opossum depredation events. Almost all (92.1%) of the eggshells were severely damaged; sometimes all that remained was a membrane with small shell fragments attached. The presence of this membrane was diagnostic of opossum depredation and was found at 65.5% of the nests destroyed by this species. An average of 3.8 damaged shells were found at nests depredated by opossums. Most eggshells (86.9%) were found within 1 meter of the nest site, but few (2.6%) were found in the nest bowl. The nest structure was usually undisturbed; only 11 (10.0%) of the 110 nests had a small to moderate amount of the nest material displaced during the depredation event.

Striped Skunk

We collected data for 77 striped skunk depredation events involving 15 individuals. Skunks typically ate

Table 2. Mean number of eggs eaten, frequency that eggshells were present, mean number of eggshells, frequency of eggshells by damage type, and distribution of eggshells by distance for depredated artificial northern bobwhite nests in Virginia, June–October 1996, where the nest predator species was known.

Species	Minimum individuals (n)	Depredation events (n)	Eggs eaten ($\bar{x}$)	Events with shells (%)	Shells left ($\bar{x}$)	Eggshells by damage type: Small holes (%)	Large holes (%)	Severe damage[a] (%)	Eggshells by distance from nest: In nest (%)	≤20 cm (%)	>20 cm–1 m (%)	>1 m (%)
Opossum	15	110	9.6	87.3	3.8	2.6	5.3	92.1	2.6	55.3	31.6	10.5
Skunk	15	77	11.7	100.0	10.1	0.9	34.7	64.4	42.6	40.6	14.8	2.0
Raccoon	10	10	9.3	10.0	4.0	0.0	25.0	75.0	0.0	75.0	25.0	0.0
Gray Fox	2	7	9.1	14.3	4.0	0.0	75.0	25.0	0.0	0.0	75.0	25.0
Dog	2	18	12.0	0.0	0.0	—	—	—	—	—	—	—
Total	44	222										

[a] Includes fractured, trampled, and crushed eggshells. See Sargeant et al. (1998) for definitions.

all eggs in the clutch, consuming an average of 11.7 of the 12 eggs available. Whole eggs were left in only 9.1% of skunk-depredated nests. Skunks usually laid down while eating an egg, holding it against the ground with their front paws and biting into the shell to release the yolk. The hole was enlarged by pushing its nose into the shell and the contents were slowly licked out.

Eggshell evidence was present at all (100.0%) skunk depredation events; an average of 10.1 shells were found at each depredated nest. Many shells (34.7%) had a large hole with fragments pressed inward, presumably where the skunk pushed its nose into the shell. Most shells (64.4%) were damaged more severely. Skunks usually ate eggs close to the nest site; 83.2% of all eggshells were less than 20 centimeters from the nest bowl. Many eggshells (42.5%) were found in the nest and few (2.0%) were found more than 1 meter away. Skunks displaced nest material at 40.3% of depredated nests and often matted the vegetation where they laid down to eat the eggs.

Raccoon

Depredation data were collected at 10 nests destroyed by 10 different raccoons. Raccoons ate most of the eggs in the clutch ($\bar{x}$ = 9.3), although whole eggs were left uneaten at 4 (40.0%) of the depredated nests. Raccoons removed eggs from the nest with their front paws and consumed them while holding the egg in an upright position. Most eggs appeared to have been ingested completely since eggshells were found at only 1 of 10 (10.0%) depredated nests. In this instance, 4 eggshells were found within 1 meter of the nest; 3 of these (75.0%) were less than 20 centimeters away. One shell had a large hole (similar to damage described for skunks) and the other 3 shells were fractured more severely. Nest material was displaced at 4 (40.0%) of 10 depredated nests.

Gray Fox

Nest depredation data were collected for 2 gray foxes that destroyed 7 nests. Foxes removed an average of 9.1 of the 12 available eggs. Whole eggs were left in 2 (28.6%) of the 7 depredated nests. All 12 eggs were missing in most (71.4%) of the nests depredated by this species. Gray foxes typically removed eggs from the nest 1 at a time, presumably to cache or consume the egg away from the nest site. The fox then returned, repeating this behavior, until all the eggs in the nest were taken.

Eggshell evidence was present at only 1 of 7 (14.3%) nests depredated by gray foxes. In most instances (57.1%), there were no eggs, shells, or shell fragments remaining at the nest site. Of the 4 eggshells found at 1 depredated nest, 3 (75.0%) had large holes and 1 (25.0%) was severely damaged. All shells were found more than 20 centimeters from the nest. No nest material displacement was observed at nests depredated by gray foxes.

Dogs

We collected depredation data for 2 dogs that destroyed 18 nests. In all instances, there were no eggs, shells, or shell fragments remaining at the nest. Dogs appeared to eat eggs at the nest site, consuming them entirely. Nest material was displaced at 50% of the nests depredated by dogs. Other dogs often visited nests but did not eat any eggs. Sometimes they ate the bobwhite wing that was covering the clutch. Of the visits involving dogs for which the number of eggs eaten could be determined (n = 40), the eggs were not consumed 42.5% of the time.

Other Species

Several other species were observed eating bobwhite eggs, but damage patterns could not be characterized because multiple species were involved in the depredation events. Four black rat snakes and 1 eastern kingsnake (*Lampropeltis getula getula*) were observed eating bobwhite eggs. On 2 occasions, a snake was found eating eggs when the nest was checked by field technicians and no photographs had been taken by the remote camera unit. Three black snakes were photographed depredating nests. A groundhog was also photographed eating bobwhite eggs. Although 3 different groundhogs were photographed 11 times at nests, only 1 individual could be confirmed as a nest predator. It appeared that this groundhog ate 3 to 4 eggs on at least 1 occasion.

DISCUSSION

The amount and type of evidence left at depredated nests is influenced by numerous factors, only 1 of which is the predator species responsible for the depredation event. Age (or size) of the predator, variation in individual behavior, presence of multiple animals (i.e., family groups), and availability of alternate food sources can all affect the manner in which a nest is preyed upon (Sargeant et al. 1998). Habitat characteristics of nest sites (density and structure of vegetation) may also affect the appearance of depredated nests and the arrangement of eggshell evidence.

Egg size affects the number of eggs eaten, extent of shell damage, distribution of eggshells, and the ability of a predator to remove an egg from the nest site. Smaller eggs are opened more easily, more likely to be transported from the nest site (Montevecchi 1976), and more likely to be consumed completely. Hernandez et al. (1997) found eggshell evidence at 93% of depredated artificial nests containing chicken eggs versus 3% when bobwhite eggs were used. Researchers should exercise caution when comparing depredation patterns described for predators destroying nests containing large eggs (Reardon 1951) with evidence left at depredated bobwhite nests.

Characteristics of nest destruction previously described for several predator species differ from those observed in this study. Stoddard (1931) reported that opossums remove bobwhite eggs 1 at a time and "gulp them down with evident relish," leaving behind little evidence to identify it as the culprit. Similarly, Darrow (1938) reported that opossums consumed the major portion of grouse eggs and left only small bits of shell. In contrast, we observed eggshell evidence at 87.3% of nests depredated by opossums, frequently with crushed membranes that were diagnostic of depredation by this species. Other evidence that strongly indicates that a nest was destroyed by an opossum includes finding fewer than 5 crushed shells scattered within 1 meter of the nest (no shells in the nest bowl) and no displaced nest material.

Raccoons also depredated bobwhite nests differently in this study compared to what researchers have reported for nests of other species. Raccoons depredating waterfowl nests typically left eggshells with large holes at the nest site (Reardon 1951, Sargeant et al. 1998). Darrow (1938) observed that raccoons usually left most of the eggshell intact when depredating grouse nests. In our study, raccoons appeared to consume entire eggs, only leaving eggshell evidence at 1 (10.0%) depredated nest. Hernandez (1995) also found no eggshell evidence at nests baited with bobwhite eggs that were depredated by raccoons, but frequently found eggshells at nests containing chicken eggs. Differences in egg size may explain these observed variations in depredation patterns. Raccoons may leave less evidence at bobwhite nests since the eggs are smaller, simpler to handle, easier to crush, and more likely to be completely consumed than waterfowl or chicken eggs. A bobwhite nest with several whole eggs left, no eggshells, and some nest material displaced is likely to have been depredated by raccoons.

We observed characteristics of nests depredated by skunks that were similar to those described by other researchers. Sowls (1948) reported that skunks bite into duck eggs and use their paws or tongue to enlarge the opening, usually crushing at least half of the shell. This crushed appearance was also noted by Darrow (1938) and Reardon (1951). Sargeant et al. (1998) found that duck eggs depredated by skunks usually had large elliptical holes that caved inward. In all these studies, including our own, the shells were not chewed up and were left close to the nest. Considerable amounts of nest material were also frequently displaced. A bobwhite nest destroyed by a skunk usually had no whole eggs remaining, many eggshells in and near the nest (frequently every depredated egg can be accounted for), and nest material was often displaced or the nearby vegetation may be trampled.

Little published information is available describing characteristics of nests destroyed by gray foxes. Nelson and Handley (1938) reported that gray foxes usually left no shell fragments, sometimes removed only a portion of the clutch, and rarely disturbed the nest structure when removing bobwhite eggs from a nest. In our study, gray foxes depredated bobwhite nests similarly. Other investigators have described depredation patterns for red foxes like those that we observed for gray foxes. In these studies, red foxes usually took all eggs from the nest, did not disturb the nest material, left no eggshell evidence, and cached the eggs away from the nest (Darrow 1938, Reardon 1951,

Sargeant et al. 1998). Although we did not locate any cached eggs at depredated nests, they could have been overlooked. Sargeant et al. (1998) reported that duck eggs cached by red foxes in enclosures were inconspicuous and located an average of 44 meters from the nest. They also reported that most incubating hens were killed and carried away from the nest to be eaten; usually only a few breast or tail feathers were left at the nest site. In our area, any nest where the incubating bird is killed and the eggs are missing is likely to have been depredated by foxes.

Domestic dogs are rarely mentioned as a nest predator of northern bobwhites or other game birds. Stoddard (1931) reported that "cur dogs" destroyed a minimum of 3% of the bobwhite nests he studied, usually leaving behind only a few pulverized eggshell fragments. Simpson (1976) could attribute only 1 of 1,092 depredated nests to dogs; in this case, the nest structure was completely destroyed and no shell fragments were found. In our study, dogs frequently visited nests but often left the eggs undisturbed. If the eggs were eaten, no eggshell evidence was left behind. The likelihood that a dog would depredate a nest is probably related to how well it was fed by its owner. Dogs might also be more likely to consume eggs containing well-developed embryos (all eggs used in this study were unincubated). Besides eating the eggs, free-roaming dogs may have detrimental impacts on nest success by harassing incubating birds and causing nest abandonment.

In some studies, snakes are implicated as the predator responsible for destroyed nests that have no physical evidence remaining at the nest site (Davis 1959, Henry 1969, Dillon 1993). Our data show that other nest predators often remove eggs or consume them whole, leaving behind no eggshells. By itself, the absence of eggshell evidence is inadequate justification for attributing nest depredation to snakes. Although numerous species of snakes have been observed depredating bobwhite nests (Stoddard 1931, Simpson 1976), studies that rely solely on a lack of eggshell evidence to conclude that a snake depredated a nest are likely biased (Hernandez 1997). Unfortunately, most investigators who report a moderate or high proportion of bobwhite nests depredated by snakes (Klimstra and Roseberry 1975, DeVos and Mueller 1993, Burger et al. 1995, Puckett et al. 1995) do not adequately describe the methods upon which their conclusions are based. Therefore, it is difficult to ascertain if snake depredation rates were overestimated in these studies.

Snakes were only infrequently observed depredating bobwhite nests in our study. However, the passive infrared sensor was probably less likely to be triggered by snakes than by mammals. Snakes often move slowly and have body temperatures similar to their environment. Of 463 depredation events that we observed, 33 (7.1%) were instances where eggs were missing, no eggshells were present, and no photograph was taken. Snakes may have been involved in some of these depredation events. The absence of an incubating bird and low egg temperatures probably reduced the likelihood that snakes would depredate our nests. In Nebraska, Glup and McDaniel (1988) reported that bullsnakes frequently destroyed waterfowl nests, but only rarely took cold eggs from abandoned nests.

Several species that were observed to be nest predators by other investigators were not observed to depredate nests in our study. Stoddard (1931) and Simpson (1976) reported that cotton rats sometimes depredated bobwhite eggs, but we could not attribute any nest predation to this species. Cotton rats were photographed 85 times at nests, but they appeared to be shell scavengers that consumed the remains of partially eaten eggs left by other predators. White-footed mice also scavenged eggshells. Other possible nest predators photographed included 3 house cats and 2 bobcats but the eggs were never eaten by these species. Stoddard (1931) reported that house cats usually killed the incubating bird but did not consume the eggs unless they contained well-developed embryos. Bobcats did not eat eggs at 5 depredated bobwhite nests in Georgia (Simpson 1976) but did consume eggs at 2 artificial bobwhite nests in Texas (Hernandez 1995). Other investigators have also reported that crows, blue jays, and turkeys (domestic and wild) occasionally destroy bobwhite nests (Stoddard 1931). However, we found no evidence that these species depredated nests that we studied, even though they were abundant and would have little difficulty locating our nests. Repeated site visits and deterioration of the nest structure after multiple depredation events made these nests easy to detect by avian predators.

Although this study provides useful data to characterize patterns of depredation for some nest predators, we do not attempt to use our results to infer which species have the greatest negative impacts. In our study, the frequency that various species depredated nests was biased, since the same individuals often depredated nests repeatedly. The absence of an incubating bird may have reduced predation rates by species that rely on olfactory cues (i.e., foxes). Also, the presence of the camera units may have caused more timid species to avoid the nests. For example, red foxes were present on the study area but were never photographed depredating nests. Red foxes are important nest predators of other species, particularly waterfowl (Sargeant et al. 1984). Other species photographed that did not depredate eggs (i.e., bobcat) may have been frightened by the camera flash or noises associated with the camera system.

Although characteristics of depredation sometimes varied among individuals of the same species, certain patterns were apparent. The presence or absence of certain characteristics can often be used to help determine which predator species are involved in depredation events (Table 3). However, many other factors (multiple predators, time elapsed since the depredation event, clutch size, incubation stage, etc.) also affect the type and amount of evidence left at depredated nests. Therefore, accurate identification of the predator species responsible will not always be possible. Researchers should recognize the importance of these factors and exercise caution when attributing nest destruction

Table 3. Characteristic evidence left at depredated northern bobwhite nests that can be used to identify the predator species most likely responsible for depredation events when observations are made within 24 hours of occurrence. Characteristic evidence descriptions are based upon authors' data and information reported by Sargeant et al. (1998).

Characteristic evidence	Most likely predator
Usually fewer than 5 eggshells present; whole eggs sometimes present; most shells severely damaged; usually one or more shells obviously chewed up with remnants consisting of membrane with small shell fragments attached; all shells usually within 1 m of nest but none in nest bowl.	opossum
All eggs eaten; 10 or more eggshells usually present; many shells with large holes and fragments pressed inward; almost all shells found within 20 cm of nest; some shells usually found in nest bowl.	striped skunk
All or most eggs missing; no shells or shell fragments present; nest material sometimes displaced; incubating bird not killed.	raccoon
All or most eggs missing; no shells or shell fragments present; cached eggs occasionally found; no nest material displaced; incubating bird frequently killed.	fox
All eggs missing; no shells or shell fragments present; nest material frequently displaced; incubating bird not killed.	dog
All or some eggs missing, no shells or shell fragments present; no nest material displaced; incubating bird usually not killed.	snake

to specific predators. Despite these limitations, we believe that predator species responsible for destroyed nests can often be identified by objectively evaluating evidence at depredated nests and combining this with information on local predator species presence and abundance.

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