

COMMENTARY

The Condor 101:718–721
© The Cooper Ornithological Society 1999

REASONS WHY PREDATORS CANNOT BE INFERRED FROM NEST REMAINS¹

SERGE LARIVIÈRE², *Département de Biologie, Pavillon Vachon, Université Laval, Ste-Foy, Québec, Canada, G1K 7P4*

Abstract. I present reasons that preclude the identification of nest predators from nest remains: inter-specific overlap and intra-specific variation in patterns of nest destruction, unexpected predators, egg size, stage of development, experience of researchers, partial nest depredation, multi-predator visits, and parental activity at depredated nests. Because many of these problems may act simultaneously, I suggest that further attempts at validating this subjective field technique be abandoned, and instead that researchers and managers invest their time and resources in objective methods of predator identification, possibly through the use of predator identification devices.

Key words: *egg remains, nest remains, nest predation, predator identification.*

Researchers often rely on the appearance of egg and nest remains to identify nest predators, a technique which evolved based on patterns of egg destruction displayed by captive animals (Darrow 1938, Sooter 1946, Sowls 1948). The ease of application of this technique, including no special effort or device required, as well as its post-mortem applicability—that is, a verdict can be pronounced even if a nest is discovered already depredated—contributed to its popularity as a field procedure (Sargeant et al. 1998). Interestingly, numerous researchers have suggested that the technique is not reliable (Trevor et al. 1991, Brown et al. 1998) and yet, the technique is still being used and tested (Hernandez et al. 1997, Mabee 1997).

Recent publications regarding this technique prompted me to carefully examine whether the tradition of identifying nest predators from nest remains is supported by scientific evidence. Herein, I provide a critique of this field method and in doing so, I present reasons why nest predators cannot, and therefore should not, be inferred from nest remains.

CONFUSING PREDATORS

The main problem impairing the identification of predators from nest remains is that numerous species share similar patterns of nest predation. For example, red fox-

es *Vulpes vulpes*, Franklin ground squirrels *Spermophilus franklinii*, raccoons *Procyon lotor*, weasels *Mustela* spp., American mink *M. vison*, crows *Corvus* spp., rats *Rattus* spp., snapping turtles *Chelydra serpentina*, and gulls *Larus* spp. have all been reported to remove entire eggs from nests of waterfowl and other waterbirds (Montevicchi 1976, Major 1991, Thorp and Clark 1994). Thus, an empty nest bowl does not permit identification of species—or taxa—responsible for its failure.

Patterns of egg breakage also greatly overlap among species, and researchers have attempted to separate patterns by publishing photographs or drawings of eggs broken by different animals (Einarsen 1956, Davis 1959). However, the photographic evidence also is controversial: the pictures published by Hernandez et al. (1997) of eggs broken by raccoons and striped skunks (*Mephitis mephitis*) are extremely similar, although both are considered as “characteristic eggshell evidence” according to the authors. Inter-specific overlap in patterns of egg breakage also is displayed for gray fox *Urocyon cinereoargenteus* (Fig. 2C in Hernandez et al. 1997) and coyote *Canis latrans* (Plate 1D in Sooter 1946), and between the bobcat *Lynx rufus* (Fig. 2D in Hernandez et al. 1997) and coyote (Plate 2B in Sooter 1946). In South America, eight of nine different mammal species left similar egg remains which did not allow specific identification (Arango-Vélez and Kattan 1997). Studies elsewhere have also reported inter-specific overlap (Hernandez et al. 1997, Sargeant et al. 1998). If species are to be differentiated based on nest remains, overlap in species patterns should be rare, not frequent as is revealed by the literature.

A second problem arises when individuals of the same species destroy eggs using several different methods. For example, Darrow (1938) reported that the striped skunk “invariably crushes the shells completely,” whereas Davis (1959) reported that “invariably the end of the egg will be opened almost as if it had hatched.” Alternatively, Larivière and Messier (1997) reported numerous dispositions of skunk depredated nests varying from complete destruction, partial depredation, eggshells moved or not, and variable disturbance of the nest bowl. Similarly, intra-specific variability in patterns of egg destruction occurs for raccoons which have been reported to disturb the nest bowl extensively by pawing (Rearden 1951) or leave the nest intact or very slightly disturbed (Hernandez et al. 1997). When studying patterns of nest depredation by gray foxes, Nelson and Handley (1938) concluded that “the fox by no means follows a set pattern in raiding nests,” whereas Hernandez et al. (1997) reported that all eggs ($n = 5$ eggs) destroyed by gray foxes shared the same characteristics. Obviously, patterns are highly variable and may be due to differences in predator size, sex and age, hunger, or even race (Darrow 1938, Einarsen 1956). This becomes confusing as the possibility of overlap with other species increases with intra-specific variability.

Inferring nest predators from nest remains also re-

¹ Received 15 December 1998. Accepted 27 April 1999.

² Current address: Ducks Unlimited Inc., One Waterfowl Way, Memphis, TN 38120, e-mail: slariviere@ducks.org

quires that one knows which animals are present. To achieve this, researchers may keep track of predators seen, track counts, or perform live-trapping surveys. However, there is always a risk of predators unaccounted for. For example, eggs of waterbirds, waterfowl, and grouse can be destroyed by "unusual" predators such as American Coots *Fulica americana*, armadillos *Dasyurus novemcinctus*, American badgers *Taxidea taxus*, Black-crowned Night Herons *Nycticorax nycticorax*, bobcats, cattle, Common Ravens *Corvus corax*, dogs *Canis familiaris*, hogs *Sus scrofa*, Moorhens *Gallinula chloropus*, muskrats *Ondatra zibethicus*, turtles, ungulates, weasels, or Wild Turkeys *Meleagris gallopavo* (Thorp and Clark 1994, Hernandez et al. 1997, Paine et al. 1997). Because of their smaller size, eggs of passerines have even more "unusual" predators such as American porcupines *Erethizon dorsatum*, black bears *Ursus americanus*, feral cats *Felis familiaris*, fishers *Martes pennanti*, Golden-fronted Woodpeckers *Melanerpes aurifrons*, snowshoe hares *Lepus americanus*, white-tailed deer *Odocoileus virginianus*, and woodchuck *Marmota monax* (Sealy 1994, Bayne et al. 1997, Darveau et al. 1997). Because these animals are rarely considered *a priori* as potential nest predators, and because patterns of egg destruction by these species are unavailable, they are seldom reported in studies relying on nest remains for predator identification.

In some cases, the location of a nest may lead researchers to rule out species which may not have access to the nest. For example, researchers monitoring nests in trees may not consider American mink or red foxes as potential predators although such species may occasionally climb trees (Sklepkovych 1994, Larivière 1996). Furthermore, overwater nests may be depredated by terrestrial species which may occasionally forage in water (American badger, Brandt 1994; striped skunk, Sullivan 1990), and island nests may be depredated by species which may swim long distances to reach these islands (American mink, Craik 1995). Very seldom can all potential predators be identified, and even if they are, the odds of overlap in patterns of nest destruction increase with diversity of the predator community.

Patterns displayed by a species may also vary according to the size of eggs in nests (Einarsen 1956, Hernandez et al. 1997). For example, crows commonly carry eggs away from nest sites, but eggs that are too large to be carried away may be consumed on location (Montevicchi 1976). Egg size may also explain why the smaller Richardson and thirteen-line ground squirrels (*Spermophilus richardsonii* and *S. tridecemlineatus*, respectively) do not prey on duck eggs, whereas the larger Franklin ground squirrel frequently does (Sargeant et al. 1987).

Again, the problem is greater with passerine nests, as even more species may break, carry, or consume entire eggs (see Marini and Melo 1998 for review of South American predators). The large Japanese quail eggs used in many nest experiments may not be broken by small mammals, and predation by small mammals may go unnoticed (Haskell 1995). Furthermore, eggs may be destroyed or removed by competitors, conspecifics, or by nest parasites (Brown and Brown 1988, Arcese et al. 1996, White and Kennedy 1997). For this reason, most studies have limited their identification of

predators to taxa, and infer mammal predation when the nest or nest site is disturbed, and bird or snake predation when the nest is not disturbed. However, even this crude segregation requires caution, especially when eggs are missing (Marini and Melo 1998).

Finally, patterns of destruction by predators may vary as eggs mature. For example, shells of eggs containing advanced embryos are often broken in smaller pieces compared to shells of fresh eggs (Darrow 1938, Einarsen 1956); therefore, researchers cannot assess whether the pattern observed is due to a different predator, or simply to the stage of development of the eggs.

Identification of predators from nest remains may become more accurate with a researcher's experience. However, inexperienced graduate students and summer assistants often perform nest visits, and observer experience, if at all present, is highly variable. For inexperienced field workers, field signs may be interpreted erroneously. For example, inexperienced field workers may confound the smell of red fox urine with the similar smell of striped skunk musk. It may be common for red foxes to urinate on depredated nests as urine acts as a "no-food" signal (Henry 1977). However, striped skunks only release musk when threatened and never do so for scent marking (Larivière and Messier 1996).

PARTIAL PREDATION AND NEST VISITATION INTERVALS

Whether a nest is found partially depredated or completely depredated depends ultimately on the time interval between consecutive visits by researchers. Thus, any species which can remove or carry eggs away from the nest site is likely to cause partial depredation. Furthermore, partial nest depredation can be caused by species which may not depredate the entire nest due to other factors such as satiation. For example, striped skunks were historically reported to destroy entire clutches (Rearden 1951), but recent research indicates that partial nest depredation is common for this species (Larivière and Messier 1997). The problem of partial predation leads to two additional problems: multi-predator visits and eggshell removal.

Multi-predator or scavenger visits are probably the most commonly overlooked limitation of the method. Nest visits are seldom performed daily to avoid causing abandonment or increased predation related to observer visits. Thus, both natural and simulated nests are typically visited every 5–14 days for most bird species (Major and Kendall 1996). During this interval, predation may occur anytime, and predation on the first day means that for the remainder of the interval, the nest contains broken eggs which may release visual and olfactory cues that are normally not present at undisturbed nests. Thus, partially or completely destroyed nests may attract scavengers and secondary predators. In Virginia, 43% of all depredated nests ($n = 114$) were visited by 2–5 species within the 7-day visit interval (Leimgruber et al. 1994). In Texas, Baker (1978) collected hairs of both skunks and raccoons at nests depredated within a 7-day interval. Similarly, over 30% of the nests visited by striped skunks in Saskatchewan, Canada, were already partially or totally depredated by other animals of the same or different species (Larivière and Messier 1997). In the Ozarks,

6.7% of clay eggs recovered from depredated passerine nests ($n = 326$) after 5 days of exposure showed signs of predation by more than one predator species (Dovon et al. 1997). Furthermore, Hernandez et al. (1997) reported that 2% of nests already depredated were visited by scavengers even within a single night. Finally, two predators may depredate the same nest simultaneously (Stanton 1944), and fighting for eggs at the nest site may add variability in the patterns observed.

Multi-predator or scavenger visits can cause great changes to the appearance of the depredated nest following departure of the initial predator. Obviously, the patterns observed by field researchers may reflect the combined action of several species of predators and scavengers, and patterns may become extremely confusing. For example, Trevor et al. (1991) reported that missing eggs were common at nests depredated by striped skunks (nests were visited every 3 days). However, striped skunks do not cache or remove eggs (Larivière and Messier 1997). In the study of Trevor et al. (1991), the action of scavengers was probably responsible for the lack of eggshells at nests depredated by skunks. In Saskatchewan, Canada, nests partially depredated by striped skunks were often completely voided of eggshells by scavengers within 4 days (Larivière and Messier 1997).

In some cases, species have been characterized or identified by the amount of yolk left in the nest bowl (Rearden 1951). However, numerous scavenger species may consume leftover yolk. For example, carrion beetles (Family Silphidae) are often found in the bottom of eggshells at partially depredated natural or simulated duck nests (Sargeant et al. 1998; S. Larivière, pers. observ.). Thus, a visit 6 days after a nest predation event may yield nothing but clean eggshells, which invalidates this criterion for the identification of nest predators.

Another problem may arise with natural nests. Nesting birds may re-arrange nest remains, or remove eggshells or entire damaged eggs from partially depredated nests, even between predator visits (Sowls 1955, Larivière and Walton 1998). Again, disposition or lack of eggshell remains at natural nests may lead researchers to believe that entire eggs have been removed from the nest when in fact, it may represent the work of the nesting hen cleaning the nest after partial depredation. Again, this would be erroneously classified if researchers were to follow the patterns reported by Rearden (1951) and others.

DISCUSSION

Putting the blame for nest predation on the wrong species may have serious and expensive consequences in wildlife management. For researchers, erroneous conclusions can be drawn and the adaptive significance of some behavioral or ecological patterns may remain unclear if true predators are misidentified.

The solution to these issues depends on the question being asked. Researchers should carefully identify the ecological question of interest concerning nest predation and consider their alternatives accordingly.

For management purposes, identifying specific predators may not be as important as identifying multi-species landscape approaches that may mitigate nest

predation without relying on species-specific management programs. Multi-purpose conservation approaches have multi-species benefits and are more likely to be supported by the public than monospecific practices. Furthermore, any mistake in the identification of the "most important" predator is not as likely to affect the efficiency of a management program based on landscape vs. species management.

In many cases however, identification of nest predators is crucial. Nest predation is a predator-prey system and a complete understanding of what is happening to the prey is strongly dependent on the behavioral ecology of nest predators. Thus, determining the primary predator species is essential to understand some aspects of nesting biology. Researchers that do not identify primary predators can only describe patterns without being able to relate them to the evolutionary pressures faced by nesting birds. Currently, one of the better alternatives remains the use of simulated nests and predator-identification devices such as haircatchers and nest cameras (Major and Kendal 1996). Simulated nests may not always experience the same survival as natural nests (Wilson et al. 1998). Similarly, predator-identification devices are not bias-free (see review in Major 1991), but using any device is still more objective and scientific than a crude guess based on the appearance and disposition of eggshell remains.

The identification of nest predators from nest remains is a good example of a procedure that was "made into a law through verbal repetition" (Romesburg 1981). Because of the lack of scientific evidence, and because of the possible biases listed above, the implementation of management programs based on this technique is unacceptable at the beginning of the 21st Century. Researchers attempting to identify nest predators should try other methods which rely on objective results instead of subjective opinions.

Ideas for this manuscript arose following field work financed by the Prairie Habitat Joint Venture through a research grant from Ducks Unlimited (Institute for Wetland and Waterfowl Research) and the Canadian Wildlife Service. I thank the University of Saskatchewan for logistic support through the early writing phases of this manuscript, and Fonds pour les Chercheurs et l'Aide à la Recherche (FCAR) for a post-doctoral fellowship which allowed its completion. N. Dion, L. R. Walton, L. Lesage, and J. Huot reviewed earlier drafts of this manuscript.

LITERATURE CITED

- ARANGO-VÉLEZ, N., AND G. H. KATTAN. 1997. Effects of forest fragmentation on experimental nest predation in Andean Cloud forest. *Biol. Conserv.* 81: 137-143.
- ARCESE, P., J. N. M. SMITH, AND M. I. HATCH. 1996. Nest predation by cowbirds and its consequences for avian demography. *Proc. Natl. Acad. Sci.* 93: 4608-4611.
- BAKER, B. W. 1978. Ecological factors affecting wild turkey nest predation on south Texas rangelands. *Proc. Annu. Conf. S.E. Assoc. Fish Wildl. Agencies* 32:126-136.
- 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.
- BRANDT, D. A. 1994. Overwater foraging by a badger. *Prairie Nat.* 26:171.
- BROWN, C. R., AND M. B. BROWN. 1988. The costs and benefits of egg destruction by conspecifics in colonial Cliff Swallows. *Auk* 105:737–748.
- BROWN, K. P., H. MOLLER, J. INNES, AND P. JANSEN. 1998. Identifying predators at nests of small birds in a New Zealand forest. *Ibis* 140:274–279.
- CRAIK, J. C. A. 1995. Effects of North American mink on the breeding success of terns and smaller gulls in west Scotland. *Seabird* 17:3–11.
- DARROW, R. 1938. Possibilities of recognizing the evidence of predation and the species involved in the remains of grouse and grouse nests found destroyed. *Trans. N. Am. Wildl. Conf.* 3:834–838.
- DARVEAU, M., L. BÉLANGER, J. HUOT, E. MÉLANÇON, AND S. DEBELLEFEUILLE. 1997. Forestry practices and the risk of bird nest predation in a boreal coniferous forest. *Ecol. Appl.* 7:572–580.
- DAVIS, J. R. 1959. A preliminary progress report on nest predation as a limiting factor in wild turkey populations. *Proc. Natl. Wild Turkey Symp.* 1: 138–145.
- DONOVAN, T. M., P. W. JONES, E. M. ANNAND, AND F. R. THOMPSON III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075.
- EINARSEN, A. S. 1956. Determination of some predator species by field signs. *Oregon State Univ. Monogr., Stud. Zool.* 10:5–34.
- HASKELL, D. G. 1995. Forest fragmentation and nest predation: are experiments with Japanese quail eggs misleading? *Auk* 112:767–770.
- HENRY, J. D. 1977. The use of urine marking in the scavenging behaviour of the red fox (*Vulpes vulpes*). *Behaviour* 61:82–106.
- HERNANDEZ, F., D. ROLLINS, AND R. CANTU. 1997. Evaluating evidence to identify ground-nest predators in west Texas. *Wildl. Soc. Bull.* 25:826–831.
- LARIVIÈRE, S. 1996. The American mink, *Mustela vison* (Carnivora, Mustelidae) can climb trees. *Mammalia* 60:485–486.
- LARIVIÈRE, S., AND F. MESSIER. 1996. Aposematic behaviour in the striped skunk, *Mephitis mephitis*. *Ethology* 102:986–992.
- LARIVIÈRE, S., AND F. MESSIER. 1997. Characteristics of waterfowl nest depredation by the striped skunk: can predators be identified from nest remains? *Am. Midl. Nat.* 137:393–396.
- LARIVIÈRE, S., AND L. R. WALTON. 1998. Eggshell removal by duck hens following partial nest depredation by striped skunk. *Prairie Nat.* 30, in press.
- LEIMGRUBER, P., W. J. MCSHEA, AND J. H. RAPPOLE. 1994. Predation on artificial nests in large forest blocks. *J. Wildl. Manage.* 58:254–260.
- MABEE, T. J. 1997. Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bull.* 109: 307–313.
- 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.
- MARINI, M. A., AND C. MELO. 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. *Condor* 100:395–399.
- MONTEVECCHI, W. A. 1976. Egg size and the egg predatory behaviour of crows. *Behaviour* 57:304–320.
- NELSON, A. L., AND C. O. HANDLEY. 1938. Behavior of gray foxes in raiding quail nests. *J. Wildl. Manage.* 2:73–78.
- PAINE, L., D. J. UNDERSANDER, D. W. SAMPLE, G. A. BARTELT, AND T. A. SCHATTEMAN. 1997. Comparison of simulated ground nest types for grazing/trampling research. *J. Range. Manage.* 50:231–233.
- REARDEN, J. D. 1951. Identification of waterfowl nest predators. *J. Wildl. Manage.* 15:386–395.
- ROMESBURG, H. C. 1981. Wildlife science: gaining reliable knowledge. *J. Wildl. Manage.* 45:293–313.
- SARGEANT, A. B., M. A. SOVADA, AND R. J. GREENWOOD. 1987. Responses of three prairie ground squirrel species, *Spermophilus franklinii*, *S. richardsonii*, and *S. tridecemlineatus*, to duck eggs. *Can. Field-Nat.* 101:95–97.
- SARGEANT, A. B., M. A. SOVADA, AND R. J. GREENWOOD. 1998. Interpreting evidence of depredation of duck nests in the prairie pothole region. U.S. Geological Survey, Northern Prairie Wildl. Res. Center, Jamestown, ND.
- SEALY, S. G. 1994. Observed acts of egg destruction, egg removal, and predation on nests of passerine birds at Delta Marsh, Manitoba. *Can. Field-Nat.* 108:41–51.
- SKLEPKOVYCH, B. 1994. Arboreal foraging by red foxes, *Vulpes vulpes*, during winter food shortage. *Can. Field-Nat.* 108:479–481.
- SOOTER, C. A. 1946. Habits of coyotes in destroying nests and eggs of waterfowl. *J. Wildl. Manage.* 10: 33–38.
- SOWLS, L. K. 1948. The Franklin's ground squirrel, *Citellus franklinii* (Sabine), and its relationship to nesting ducks. *J. Mammal.* 29:113–137.
- SOWLS, L. K. 1955. Prairie ducks: a study of their behavior, ecology and management. Stackpole, Harrisburg, PA.
- STANTON, F. W. 1944. Douglas ground squirrel as a predator on nests of upland game birds in Oregon. *J. Wildl. Manage.* 8:153–161.
- SULLIVAN, B. D. 1990. Striped skunk swims to overwater duck nest. *Prairie Nat.* 22:271–272.
- THORP, T. J., AND L. S. CLARK. 1994. Common snapping turtle eats duck eggs. *Wilson Bull.* 106:416.
- TREVOR, J. T., R. W. SEABLOOM AND R. D. SAYLER. 1991. Identification of mammalian predators at artificial waterfowl nests. *Prairie Nat.* 23:93–99.
- WHITE, D. W., AND E. D. KENNEDY. 1997. Effect of egg covering and habitat on nest destruction by House Wrens. *Condor* 99:873–879.
- 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.