Temporal Patterns of Predation of Duck Nests in the Canadian Prairies

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ABSTRACT.—In 1995 we deployed 800 simulated nests equipped with nest mortality timers to assess temporal patterns of predation of duck nests in the Canadian prairies. Timers recorded 470 predation events (70% of 672 depredated nests). Predation was nonrandom throughout the day, with a peak occurring between 00:00 and 06:00. Coyote (Canis latrans) and red fox (Vulpes vulpes) depredated nests at similar times (mean 18:32 and 22:42, respectively), whereas mean depredation time was significantly later for striped skunks (Mephitis mephitis, 02:08). We failed to detect a difference in depredation interval for neighboring nests destroyed by striped skunk (median = 62 h 18 min, n = 15) vs. pairs of nests depredated by different species (red fox-skunk, skunk-coyote and coyote-red fox, median depredation interval = 123 h 1 min, n = 6). Simultaneous observation of radio-marked skunks revealed that skunks spent 2–25 min at simulated nests and became inactive after nest destruction in ca. 50% of cases. Based on observations of striped skunk behavior and nest-timer data, we suggest that density-dependent nest predation is caused by increased patch use rather than area-restricted search.

INTRODUCTION

Nest predation is the most important proximate factor influencing duck numbers (Klett et al., 1988; Greenwood et al., 1995). Consequently, researchers have studied how factors such as habitat characteristics (Pasitchniak-Arts and Messier, 1995a; Sovada et al., 2000) or nest density (Larivière and Messier, 1998a) affect spatial patterns of predation of duck nests. In many cases, simulated nests are used to test hypotheses. Simulated nests often do not reflect the success of natural nests (Wilson et al., 1998). However, they enable researchers to perform controlled experiments with efficient designs and large samples and they facilitate predator identification (Major and Kendal, 1996).

Recently, the use of timing devices (small clocks hidden at the nest with an egg resting on a stop switch) at simulated nests has allowed researchers to establish temporal patterns of nest predation (Ball et al., 1994; Bayne and Hobson, 1997). However, timers also can be used to test assumptions about predator behavior following depredation of nests. For example, researchers suggest that density-dependent nest predation is observed when predators display area-restricted search following depredation of a nest (O’Reilly and Hannon, 1989; Niemuth and Boyce, 1995). Area-restricted search is defined as an immediate increase in foraging activity around the area where a food item was found (Tinbergen et al., 1967). When predators exhibit area-restricted search, food items are more likely to be depredated if a nearby item has been depredated. For ground-nesting ducks there is evidence that at extremely high nest densities (>10 nests/ha), density-dependent predation occurs and the fate of a nest is affected by the fate of its nearest neighbor (Larivière and Messier, 1998a). However, density dependence does not confirm that predators display area-restricted search. An alternative hypothesis is that density-dependent nest predation and nearest neighbor

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effects occur because high densities of nests, as well as sensory cues from depredated nests, attract more predators to the area.

Herein, we used timers to: (1) assess temporal patterns of predation on duck nests in the Canadian prairies and (2) test whether nest predators exhibit area-restricted search following depredation of simulated nests. Finally, we contrast data from the nest experiment with direct observation of free-ranging striped skunks (Mephitis mephitis) to corroborate information obtained from nest timers.

**STUDY AREA**

We conducted this study near Krydor, southcentral Saskatchewan (52°45’N, 107°08’W) during May–July 1995. Grain (i.e., wheat, barley, oats) and oil crops (canola and flax) occupy 60% of the landscape. Topography is gently rolling, and an extensive network of roads divides the land. The area is typical of the parklands: numerous wetlands and stands of trembling aspen (Populus tremuloides) occur throughout the region. Other characteristics of the prairie parklands are provided by Greenwood et al. (1995).

In this area the striped skunk is one of the principal predators of duck eggs (Pasitschniak-Arts and Messier, 1995b); red foxes (Vulpes vulpes), raccoons (Procyon lotor), American badgers (Taxidea taxus) and coyotes (Canis latrans) also occur. Birds such as black-billed magpies (Pica pica) and American crows (Corvus brachyrhynchos) are present but their importance as egg predators is marginal (Pasitschniak-Arts and Messier, 1995b).

**METHODS**

**Simulated nest experiment.**—We used a randomized block design to deploy simulated nests because our primary goal was to test whether density-dependent predation and nearest-neighbor effects occurred at high nest densities (Larivière and Messier, 1998a). Each block (n = 5 replicates) consisted of a quarter section (800 m × 800 m) of managed nesting cover. Within each block, we positioned three treatment quadrats (2–4 ha) with densities of 2.5, 10 and 25 simulated nests/ha. Within each quadrat we randomly selected nest locations, with the constraint that nests must be >5 m apart, but we did not estimate the density of natural nests. Simulated nests consisted of six chicken eggs deposited in a small (15-cm diam) depression in the ground and covered with dead vegetation. At each nest we positioned one egg on a timing device (modified from Ball et al., 1994). Our timing devices consisted of stopwatch glued to a 4-inch nail (to provide stability of the clock) with an egg placed on the stop switch. Clocks were adjusted to current time, and removal of the egg from the switch (following depredation) stopped the clock and recorded the time of depredation.

Nests were constructed on 15 May 1995 and visited every 5 d for 25 d. The experiment was repeated on 15 June. A nest was considered depredated when ≥1 egg was damaged or missing.

We compared recorded times of predation by skunks with observed cases of predation at simulated nests during radio-tracking of skunks (Larivière and Messier, 1997a). Recorded times were judged accurate if the skunk was at the nest during the recorded time ± 5 min.

**Predator identification.**—We used haircatchers (Pasitschniak-Arts and Messier, 1995b) to collect mammalian hairs at depredated nests. Hairs were subsequently identified using scale patterns (Moore et al., 1974; Adorjan and Kolenosky, 1980).

**Testing the area-restricted search behavior:**—For each pair of neighboring nests at which both hair samples and depredation times were recorded, we measured the time interval between depredation events. We hypothesized that if nest predators displayed area-restricted search, then depredation interval for neighboring nests destroyed by the same species would
be shorter than for nests depredated by different species. We also predicted that if animals displayed area-restricted search, then most pairs of neighboring nests would be depredated within a few hours of each other, or at least within the same night. This prediction was made based on the fact that skunks typically remain at a nest $\leq 45$ min (Lariviére and Messier, 1997a).

**Capture of skunks and radio-tracking protocol.**—Captured skunks were immobilized with halothane and Telazol® (Lariviére and Messier, 1996a, b) and equipped with motion-sensitive radiocollars (150–152 Mhz, Telonics Inc., Mesa, Ariz.).

At night each observer followed, on foot, one radiocollared skunk, locating the animal by direct observation or short-range (<50 m) triangulation every 15 min from 18:00 to 06:00 (Lariviére and Messier, 1998b). We used night-vision goggles (AN-PVS 5, Bill’s Electronics, Mildmay, ON) to directly observe skunks during tracking sessions (Lariviére and Messier, 1998b).

**RESULTS**

Eight female and 1 male striped skunk were captured. Although we equipped all 9 animals with radiocollars, 1 male and 1 female relocated outside the study area. We radio-tracked the remaining 7 females for 795 h.

**Daily patterns of nest depredation.**—Overall, predators destroyed 672 of 800 simulated nests (84%). Timers recorded depredation times in 470 instances (70% of depredated nests), and predator hairs were identified at 132 (28%) of these nests: striped skunks, red fox, coyote and raccoon depredated 93, 19, 17 and 3 nests, respectively. Because of only 3 data points, raccoons were not considered further.

Circular statistics (Zar, 1984) revealed that daily patterns of nest destruction did not differ (Watson’s F-test for two circular means, $F = 0.3$, $P = 0.58$) between May (mean depredation time = 02:48, $n = 183$ timed events) and June (mean depredation time = 02:18, $n = 287$ timed events). Thus, we pooled all nests for further analyses.

Nest predation was not distributed uniformly throughout the day (Rayleigh’s test of uniformity, $R = 68.2$, $P < 0.01$, $n = 470$). Most predation events occurred between 00:00 and 06:00 (Fig. 1A). Mean depredation times ($\pm SD$) for nests destroyed by coyote, red fox and striped skunk were 18:32 ± 7 h 8 min, 22:42 ± 5 h 51 min, and 02:08 ± 5 h, respectively (Fig. 1B-D). Considering only nests for which predators were identified, the mean depredation time of nests destroyed by fox and coyote did not differ ($F = 2.5$, $P = 0.13$). However, there was a difference in mean time of depredation for nests destroyed by fox and skunk (Watson’s F-test with Bonferroni corrections, $F = 4.8$, $P = 0.03$) and by coyote and skunk ($F = 10.3$, $P < 0.01$).

Area-restricted search.—We obtained depredation times for 27 pairs of destroyed adjacent nests, including 21 pairs for which predators were identified at both nests. Of those, 15 pairs were depredated by skunks and the remaining pairs were destroyed by fox-skunk (4 pairs), skunk-coyote (1 pair) and coyote-fox (1 pair). There was no difference (Mann-Whitney U-test, $n_{\text{skk-akk pairs}} = 15$, $n_{\text{other pairs}} = 6$, $Z = -0.9$, $P = 0.38$) in median time interval between pairs of nests depredated by skunks (median = 62 h 18 min, range = 21 min–16 d, $n = 15$) vs. pairs of nests depredated by two species (median = 123 h 1 min, range = 71 min–10 d, $n = 6$). Only two of fifteen nearest neighbor nests depredated by skunks were destroyed within 60 min; other pairs were destroyed within 12 h ($n = 2$), within 48 h ($n = 2$) or $>48$ h apart ($n = 9$).

Behavior of striped skunks following nest depredation.—We observed depredation of 16 simulated nests (5, 4 and 7 in low, medium and high nest density quadrats, respectively) and 7 natural duck nests by 5 female striped skunks during 795 h of nighttime radio-
tracking. Upon encountering the nest, skunks spent from 2–25 min (median = 11 min, \( n = 16 \)) at a simulated nest. Time spent at simulated nests was lower (one-tailed Mann-Whitney U-test, \( Z = -2.22, P = 0.01 \)) for nests previously depredated (median = 3 min, range 2–11 min, \( n = 5 \)) than for intact nests (median = 18 min, range 3–25 min, \( n = 11 \)). Twelve of the 23 encounters (6/7 for natural nests, 6/16 for simulated nests) were followed by a
period of inactivity either in the vicinity (<20 m) of the depredated nest (3 cases) or at
the maternal den usually <2 km away (9 cases).

The 23 observed depredation events occurred during 15 separate radio-tracking sessions. We
radiotracked the same individual skunk the night after predation in 9/15 cases. In 8/9 cases, the skunk
returned to the same experimental block of habitat where a nest had been depredated the night before, but did not necessarily revisit the exact density quadrat where depredation had occurred. In three of those eight instances, the skunk returned to
a nest that it had partially depredated the previous night.

Nest timers recorded times within the interval of time spent at the nest by the skunk in
8/16 cases of observed depredation of simulated nests. Three timers stopped functioning and five timers reported times before observed nest depredation events (average time dif-
ference = 33 h 12 min, SD = 14 h 0 min), suggesting depredation by another individual
or by another species had already occurred. Interestingly, we collected hair samples at only
8/16 simulated nests where we directly observed depredation by skunks; seven hair samples
were correctly classified as striped skunk and one hair sample was classified as unknown.

DISCUSSION

In this study we used nest timers not only to determine temporal patterns of predation,
but also to test whether depredation events between nearest neighboring nests were tem-
porally independent. Our results indicate that neighboring nests were only occasionally
destroyed within 1 h of each other. Moreover, striped skunks often rested following dep-
redation of nests and neighboring nests frequently were depredated by different species of
predators. Thus, the fate of nearest neighbor nests may be linked because of their position
within a field (Larivièere and Messier, 1998a), but their respective fates remain temporally
independent.

Striped skunks are small predators that depredate nests opportunistically (Larivièere and
Messier, 1997a). Although we observed a single skunk depredate up to 4 duck nests and
destroy up to 14 eggs within a single night (Larivièere and Messier, 1997a), skunks often
leave abundant egg yolk inside egg shells, showing that all eggs are not entirely consumed.
Most often, skunks destroy <6 eggs when encountering a duck nest (Larivièere and Messier,
1997a; Larivièere and Walton, 1998), probably because of satiation. This is further supported
by frequent observations of partial nest depredation (Larivièere and Messier, 1997a, 1998a),
and our observations of skunks resting near partially depredated nests (Larivièere and Wal-
ton, 1998). Skunks at or near satiation may benefit from resting or, for females, from return-
ting to their maternal den where the progeny are located (Larivièere and Messier,
1997b). Alternatively, satiated skunks may remain active to assess food abundance in various
habitats. In either case, nearest-neighbor effects become temporally independent. Thus,
instead of displaying area-restricted search, predators may “recognize” high-density patches
where nest encounters are more frequent and increase patch use over the next few days or
weeks (Larivièere and Messier, 1998a). Skunks also may develop search images (Nams, 1991,
1997) and possibly become more successful at finding nests. Finally, the release of olfactory
and visual cues (i.e., broken eggshells, exposed yolk/blood) at depredated nests may ad-
vertise patch profitability to new predators and cause nearest neighbor effects by attracting
different predators of the same or different species.

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