IDENTIFYING PREDATORS AND FATES OF GRASSLAND PASSERINE NESTS USING MINIATURE VIDEO CAMERAS

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Abstract: Nest fates, causes of nest failure, and identities of nest predators are difficult to determine for grassland passerines. We developed a miniature video-camera system for use in grasslands and deployed it at 69 nests of 10 passerine species in North Dakota during 1996–97. Abandonment rates were higher at nests <1 day after camera deployment (23%) than <1 day after nests were found (2%, $P = 0.001$). Most birds returned to nests ≤30 min after camera deployment, but clay-colored sparrows (*Spizella pallida*) took longer to return to nests than other species ($P = 0.035$). Cameras did not appear to increase nest predation rates. We videotaped predation by ≥11 species at 29 nests: eggs or nestlings were destroyed by mice, ground squirrels, weasel, badgers, canids, deer, cowbirds, and hawks. All eggs or nestlings were removed in <15 min at 14 depredated nests. Contents were removed during >1 day or night (22–116 hr) at 6 nests, 5 of which were depredated by ground squirrels or mice. For nests without cameras, estimated predation rates were lower for ground nests than aboveground nests ($P = 0.055$), but did not differ between open and covered nests ($P = 0.74$). Open and covered nests differed, however, when predation risk (estimated by initial-predation rate) was examined separately for day and night using camera-monitored nests; the frequency of initial predations that occurred during the day was higher for open nests than covered nests ($P = 0.015$). Thus, vulnerability of some nest types may depend on the relative importance of nocturnal and diurnal predators. Predation risk increased with nestling age from 0 to 8 days ($P = 0.07$). Up to 15% of fates assigned to camera-monitored nests were wrong when based solely on evidence that would have been available from periodic nest visits. There was no evidence of disturbance at nearly half the depredated nests, including all 5 depredated by large mammals. Overlap in types of sign left by different predator species, and variability of sign within species, suggests that evidence at nests is unreliable for identifying predators of grassland passerines.

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Populations of many grassland passerines have declined in North America in recent decades (Peterjohn and Sauer 1993, Knopf 1994, Herkert 1995, Igl and Johnson 1997). Nest predation may contribute to these declines (Basore et al. 1986) or limit population recovery. Predation rates may vary widely among areas with different predator communities (Miller and Knight 1993). Loss and fragmentation of nesting habitat may increase levels of predation on grassland bird nests (Johnson and Temple 1990), but the effect of habitat fragmentation may depend on the composition of the local predator community (Nour et al. 1993). To understand why predation rates vary and how habitat features interact with predation, we must be able to accurately assess causes of nest failure and identify nest predators of grassland passerines.

Direct observations of predators at passerine nests are rare (Pettingill 1976, Sealy 1994) and may be biased toward diurnal and slower-moving predator species. Indirect evidence at the nest is of limited value because predators of passerine nests often leave little or no sign (Custer 1973, Hussell 1974, Major and Gowing 1994, Hernandez et al. 1997*a*). Limited sign increases the difficulty of determining nest fates, causes of nest failure, and identity of predators. Nevertheless, sign has been used by many researchers to attribute nest failures to various types of predators (Best 1978, Wray et al. 1982, Moors 1983, Vickery et al. 1992, Christman and Dhondt 1997). This procedure may be adequate when researchers have considerable knowledge of the predator community, but extrapolating to areas where predator communities differ can lead to errors (Brown et al. 1998). Furthermore, direct evidence linking sign left at nests with specific predators is largely lacking for grassland passerines.

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A variety of camera systems have been used to document predation and other activities at nests in woody habitats (Innes et al. 1994, Major and Gowing 1994, Franzreb and Hanula 1995, Sykes et al. 1995, Dearborn 1996, Kristan et al. 1996). Most of these systems are unsuitable for use in grasslands where cameras must be very close to nests to avoid having the view obscured by vegetation. These systems generally have large cameras and mounting systems that would be readily visible near grassland nests and could affect rates of abandonment, predation, and brood parasitism. In addition, systems with still-frame cameras generally use tripping devices and artificial flash that could disrupt parental behavior at such short distances.

Many researchers have avoided the difficulties associated with studying natural nests by using artificial nests to study predation (Major and Kendal 1996). Artificial nests connected to still cameras (Picman 1987, Savidge and Seibert 1988, Reitsma et al. 1990, Danielson et al. 1996) and–or containing plasticine eggs (Møller 1989, Nour et al. 1993, Bayne et al. 1997, Rogers et al. 1997, Hannon and Cotterill 1998) have been used to identify egg predators in a variety of habitats. However, factors that differ between artificial and natural nests, such as egg size or type (Haskell 1995, DeGraaf and Maier 1996, Bayne et al. 1997), nest appearance (Martin 1987), scent, and presence of adult birds (MacIvor et al. 1990, Sloan et al. 1998, Wilson et al. 1998) likely affect the species composition of their nest predators. Given the potential biases in predation studies that use artificial nests, Martin (1987:928) expressed the need for "direct determination of nest predators and their relative importance in nest predation."

In 1995–96, we worked with electronics specialists to develop a camera system specifically designed to monitor predation and other events at grassland passerine nests. We conducted field evaluations of prototype camera systems in 1996 and 1997, deploying cameras at nests of 10 species of grassland passerines in North Dakota. In this paper we present (1) a description of the camera system; (2) results of our camera evaluations; (3) egg, nestling, and nest fates and causes of nest failure at camera-monitored nests; (4) identities of predators and timing of predation events videotaped at nests; (5) documentation of sign left at nests by known predators; (6) a comparison of predation rates by nest stage, type, and height; and (7) an assessment of the accuracy of assigning nest fates, causes of nest failure, and predator types using conventional methods.

STUDY AREAS

Cameras were used to monitor passerine nests in a variety of grassland habitats in Stutsman and Barnes Counties, North Dakota. We monitored nests on 8 grassland sites 10–30 km from Jamestown (46°54′N, 98°42′W) in 1996, and on 14 sites 3–20 km from Woodworth (47°09′N, 99°23′W) in 1997. Most sites were public lands managed by the U.S. Fish and Wildlife Service; 6 were privately owned pastureland or retired cropland that had been planted to perennial grass. Vegetation included native and introduced species that had been subjected to various management practices (idle, hayed, grazed, burned); all fields were idle during our study. Most sites used in 1996 were dominated by grasses 30–80 cm tall; 1 site was dominated by forbs (*Melilotus* sp., *Artemisia* sp.) >1 m high. Sites used in 1997 were dominated by short to medium grasses (5–45 cm tall in late summer) with 0–20% forb cover, 0–25% shrub cover (mostly *Symphoricarpos* spp.), and 0–25 cm of litter. In 1997, habitat blocks were larger and more isolated from human activity.

METHODS

Camera System Design

We chose video recording because (1) sensors used as tripping devices for still-frame cameras are likely to be activated by vegetation, parent birds, and other non-target objects; (2) shutter sounds and camera flashes can affect predation events; and (3) single images may fail to distinguish between predators and non-predatory visitors of nests. We recorded continuously because using a tripping mechanism to start the VCR results in a delay long enough to completely miss some events at the nest (Franzreb and Hanula 1995). We used 24-hr time-lapse recording because it provided about 4–5 images/sec, which we believed would capture even the fastest predation events.

Prototype camera systems were built by J. Christensen (Christensen Designs, Manteca, California), R. Fuhrman (Fuhrman Diversified, Seabrook, Texas), and D. Garcelon (Institute for Wildlife Studies, Arcata, California). Use of company names does not imply endorsement by the U.S. Geological Survey. Each system in-

cluded a miniature black-and-white electronic-board camera in a waterproof housing with infrared (940–950 nm) light-emitting diodes around the lens to provide cryptic illumination at night. Camera lenses had fixed focal lengths of 3–4 mm with 51–88° horizontal field of view. Camera housings were cuboid or cylindrical, about 4 cm across, with volumes of 43–93 cm^3. Most cameras were mounted on a wooden dowel that was pushed into the ground; an adjustable bracket allowed the camera to be positioned quickly. Cameras were typically 10–30 cm from nest contents. The camera was connected by 40–50 m of cable to a DC-powered time-lapse VCR (Panasonic model AG-1070DC) and a deep-cycle marine battery (120 amp-hr). An interface box (8 × 5 × 3 cm) with a connector for a portable video monitor was located 0.5–1.75 m from the nest to aid camera placement. The VCR was housed in a waterproof case with external connectors for the camera, battery, and portable monitor.

Data Collection

A crew of 3 (1996) to 6 (1997) people searched for nests from sunrise to early afternoon by systematically walking through fields swinging 2-m poles or dragging a 20-m rope to flush birds. Species, status, and location were recorded for each active passerine nest that was found; eggs were candled (Lokemoen and Koford 1996) and nestling ages were estimated (0 = day of hatch) to predict hatching and fledging dates. Nests were classified by height (on or above ground level) and type (open or covered by vegetation). A small flag was placed 4 m north of each nest. Nests without cameras were checked on estimated hatching and fledging dates, or at least once per week.

Cameras were deployed at a sample of nests. We tried to select representative numbers of nests (1) at egg and nestling stages, (2) on and above the ground, (3) on each area searched, and (4) for each nesting species. Daily visits were made to each VCR to check nest status (using a portable monitor), change tapes, and check battery power. The battery was changed about every 3 days. Each camera was left in place until the nest was destroyed, abandoned, or fledged young.

When a nest with or without a camera was no longer attended by adult birds, we searched for evidence of predation (damage to the nest; eggshell fragments, prey remains, disturbed vegetation, scats, etc. ≤1 m from the nest) and fledging (feather sheaths in the nest, fledglings or alarm-calling adults nearby). Nests were considered hatched if ≥1 egg hatched, and fledged if ≥1 nestling left the nest. Nests that failed were classified as abandoned (≥1 host egg or nestling remaining in unattended nest) or destroyed. Causes of failure were classified as predation, brood parasitism, observer interference, nest tipovers, starvation, or unknown. For the sake of simplicity, animals responsible for egg or nestling losses were referred to as predators (and the losses predation) even if they did not consume what they removed or destroyed.

Data Analysis

We assessed passerine response to cameras near their nests by comparing the proportion of camera nests that were abandoned <1 day after camera deployment to the proportion of nests without cameras that were abandoned <1 day after they were located and marked. For non-abandoned camera nests, we also calculated the length of time elapsed until an adult perched or sat on the nest following camera deployment (hereafter, return time). We used a 2-sample Kolmogorov-Smirnov test to compare distributions of return times between clay-colored sparrows (the only species with an adequate sample to treat separately) and all other species combined (see Table 1 for scientific names of nesting species).

We calculated Mayfield daily survival and predation rates (Mayfield 1961, 1975; Johnson 1979) for nests with and without cameras. Egg-laying days and the day a nest was found or a camera deployed were not included as exposure days. To test the effect of cameras, we assessed exposure days and fates of camera nests following the same protocol used for nests without cameras. For camera nests, information that would have been recorded during a scheduled nest visit was obtained by viewing a sample of videotape from the appropriate day (hereafter, simulated nest visit). When a mortality occurred between nest visits, the midpoint of the interval was used as the day of mortality. We used daily survival and predation rates with Sauer and Williams (1989) χ^2 procedure to test non-camera nests for effects of nest stage (incubation or nestling), height, and type, and to compare nests with and without cameras for effects of 1 treatment (camera) and 2 classification (stage, height) variables.

Table 1. Number of nests monitored with and without cameras and exposure days used for survival analyses of grassland passerine nests in Stutsman and Barnes Counties, North Dakota, 1996–97.

	Camera			No camera		
		Exposure days[a]			Exposure days[b]	
Species	Nests	Incubation	Nestling	Nests	Incubation	Nestling
Sedge wren (*Cistothorus platensis*)	0			1	6.0	13.0
Sprague's pipit (*Anthus spragueii*)	0			1	1.0	12.0
Common yellowthroat (*Geothlypis trichas*)	1	7.0	3.0	1	5.0	10.0
Clay-colored sparrow (*Spizella pallida*)	34	36.0	96.5	186	750.0	758.0
Vesper sparrow (*Pooecetes gramineus*)	1	3.0	0.0	1	2.0	0.0
Savannah sparrow (*Passerculus sandwichensis*)	7	17.0	42.0	18	30.0	85.0
Grasshopper sparrow (*Ammodramus savannarum*)	4	0.0	23.0	6	20.0	24.0
Baird's sparrow (*Ammodramus bairdii*)	3	0.0	10.5	4	1.0	25.5
Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*)	0			1	2.0	10.0
Song sparrow (*Melospiza melodia*)	2	2.5	9.0	8	28.5	18.0
Chestnut-collared longspur (*Calcarius ornatus*)	9	22.0	37.5	47	217.0	277.5
Bobolink (*Dolichonyx oryzivorus*)	5	16.0	33.0	17	116.5	90.0
Western meadowlark (*Sturnella neglecta*)	3	1.0	3.0	4	17.0	17.0
Total	69	104.5	257.5	295	1196.0	1340.0

[a] Exposure days calculated as if nests were on the same visitation schedule as nests without cameras.
[b] Some exposure days are from nests that were subsequently monitored with cameras.

To evaluate the accuracy of assigning nest fates using information from nest visits, we compared actual fates of camera nests to fates assigned using simulated nest visits and observed sign. We also compared actual and simulated fates of eggs and nestlings, and actual and simulated daily survival rates.

We used data from camera nests to examine effects of nest characteristics on predator risk during day and night. In most calculations of predation rate, a nest is not considered depredated until the last viable egg or nestling is removed. As a measure of predation risk, we were interested in when the first egg or nestling was removed. We therefore calculated initial-predation rate based on nests that had not been depredated previously. Initial-predation rate was calculated by dividing the number of nests with predation by the number of exposure days accrued at successful nests and at depredated nests before the first egg or nestling loss occurred. We classified initial predation events as diurnal (after sunrise, before sunset) or nocturnal, and used χ^2 tests to examine initial-predation rate by nest stage, height, type, and day–night category.

We used Spearman's rank correlation to assess the association between nestling age (using oldest nestling) and initial-predation rate and survival rate calculated for each day (Pollock et al 1989). We only used nestling ages 0–8 days because most young fledged by 9 days and sample sizes beyond 8 days were limited.

RESULTS

During 1996 and 1997, we monitored fates of 364 nests of 13 passerine species (Table 1); 279 nests contained eggs and 85 contained nestlings when found. Cameras were deployed at 69 nests of 10 passerine species. At the time of camera deployment, 48 nests contained eggs, 6 were hatching, and 15 contained nestlings.

Response of Nesting Passerines to Cameras

Sixteen (23%) of 69 nests were abandoned <1 day after camera deployment. Abandonment rate was lower for 363 nests without cameras (χ^2_1 = 51.99, P = 0.001), only 7 (2%) of which appeared to be abandoned <1 day after they were found. The actual abandonment rate for non-camera nests may be higher if some abandoned nests were scavenged and misclassified as depredated. For camera nests, abandonment was related to nest stage (χ^2_1 = 5.76, P = 0.02), with only 1 abandonment occurring after hatch. Abandonments at camera nests were not restricted to any species, nest type, nest height, study site, camera type, camera distance from nest, or date or hour of camera deployment. In 1996, 3 (18%) of 17 camera nests were abandoned; in 1997, 13 (25%) of 52 were abandoned.

At 51% of 49 non-abandoned nests for which return times were measured, an adult returned to the nest in ≤30 min of camera deployment; at 76% of nests, an adult returned in ≤60 min. Return times to 11 of 38 nests in 1997 were longer than the longest return time in 1996 (61 min). The cumulative distribution function of return times differed (D = 0.385, P = 0.035) between clay-colored sparrows and other species. Clay-colored sparrows accounted for all 8 nests where adults were absent for >90 min after camera deployment. Absences of 26 clay-colored sparrows ranged from 1 min to 11.4 hr. Those absent for several hours returned just before dark; thus, the earlier in the day the camera was deployed, the longer the nest was unattended.

Egg, Nestling, and Nest Fates

Fates of eggs and nestlings were determined for 47 of 53 camera nests that were not abandoned (Tables 2 and 3); at the other 6 nests, equipment failed or (in 2 cases) was removed before nest completion. Of the 45 nests monitored during incubation that had known fates, 51% hatched (Table 2). Of the 41 nests monitored after hatching that had known fates, 56–68% fledged young (Table 3). At 6 nests, we documented ≥1 young departing the nest during or immediately after depredation of its nest mate(s) (hereafter, forced fledging). The percentage of nests classified as successful depends on whether forced fledgings are accepted as fledged. These young were within a day of minimum ages considered normal for fledging. In 1 case, however, videotape showed that the fledgling was caught and eaten by the predator just outside the nest.

We documented many events that could lead to errors when nest fates and causes of failure are assigned using information from periodic nest visits. Examples include (1) fledgings induced by predators at 6 nests; (2) 2 aboveground nests that gradually tipped over, dumping nestlings on the ground; (3) a parent that

Table 2. Videotaped fates of eggs and nests during incubation for 10 grassland passerine species in Stutsman and Barnes Counties, North Dakota, 1996–97.

		No. eggs					
Nest fate	No. nests	Hatched	Dead[a]	Depredated	Abandoned	Unknown	Total
Hatched	23	85	8	2	0	0	95
Depredated	7	0		25	0	0	25
Abandoned	15	0		8[b]	52	0	60
Censored[c]	3					13	13
Total	48	85	8	35	52	13	193

[a] Infertile or dead embryo.
[b] Eggs destroyed by cowbirds at unattended nests.
[c] Camera system failed (n = 2) or removed (n = 1) before predicted hatch date.

knocked 2 2-day-old nestlings out of the nest when it flushed at night; (4) a red fox (see Table 6 for scientific names of predators) scavenging eggs that had been punctured by a brown-headed cowbird; (5) removal of 3 eggs from 1 nest by a cowbird(s) that laid no parasitic eggs; and (6) a thirteen-lined ground squirrel killing and removing a parent from the nest.

Based on information from simulated nest visits, we correctly determined fates of 40 of 47 nests (22 fledged, 17 depredated, 1 apparent starvation). For 2 of the depredated nests, however, the stage at which predation occurred was incorrectly assigned to incubation rather than nestling stage.

Fates of ≤7 (15%) of 47 nests could have been misclassified using nest visits. For 5 nests in which all fledgings were forced by predators, 3 were classified as fledged and 2 were classified as depredated. For 1 of the nests classified as fledged, videotape indicated that no young survived. Of the 2 nests that tipped over, 1 fledged young but was classified as depredated; the other would have been classified as depredated or as destroyed due to unknown causes, depending on whether or not the young were scavenged before a nest inspection occurred.

Despite these errors, estimates of daily survival rates were similar when calculated using actual nest fates and using nest fates assigned from simulated nest visits (Table 4). For the incubation stage, the simulated sample included 2 more mortalities than the actual sample but a similar number of exposure days. For the nestling stage, the simulated and actual samples had a similar number of mortalities, but the actual sample included more exposure days because predation events often occurred after the mid-point between nest visits.

Fates of 138 nestlings from 40 non-abandoned nests were recorded on videotape. Using information from simulated nest visits, 67 of these were correctly classified as fledged and 49 were correctly classified as depredated. Fates of ≤22 nestlings (16%) could have been misclassified using information from nest visits. Four nestlings that were force fledged were classified as depredated and 4 were classified as fledged. Eight depredated nestlings were classified as fledged. One nestling that fledged from a tipped nest was classified as depredated; 5 others that died after falling out of tipped nests would have been classified as depredated or as destroyed due to unknown causes.

Daily Survival and Predation Rates

For nests without cameras, Mayfield survival rates were higher (χ^2_1 = 6.42, P = 0.011) and predation rates lower (χ^2_1 = 3.68, P = 0.055) for ground nests than for aboveground nests. Nest losses other than predation (i.e., mortality rates excluding predation) also were lower for ground nests (χ^2_1 = 9.25, P = 0.002). Survival rates were not related to nest stage (χ^2_1 = 0.44, P = 0.51), but predation rates tended to be lower on eggs than nestlings (χ^2_1 = 2.45, P = 0.12). We detected no difference in survival (χ^2_1 = 0.11, P = 0.74) or predation rates (χ^2_1 = 0.00, P = 0.98) between open and covered nests. We found no evidence of interactions of nest stage, height, and type (χ^2_1 = 0.33–3.22, P = 0.20–0.85).

When testing for camera effects on daily survival and predation rates, we found evidence of a 3-way interaction among nest stage, height, and camera presence for predation rates (χ^2_1 = 4.49, P = 0.034) and survival rates (χ^2_1 = 2.82, P = 0.093). The interaction resulted from the high predation rate estimated for aboveground camera nests during incubation (Fig. 1). For this group, the number of exposure days (36) was too small to provide reliable estimates. Af-

Table 3. Videotaped fates of hatched nests and nestlings for 9 grassland passerine species in Stutsman and Barnes Counties, North Dakota, 1996–97.

		No. nestlings							
		Fledged		Died					
Nest fate	No. nests	Normal	Forced[a]	Depredated	Fell out	Starved	Abandoned	Unknown	Total
Fledged[b]	23	67[c]	1	7	1	0	0	1	77
Force fledged	5	0	7	8	0	0	0	0	15
Depredated	10	0	0	38	0	0	0	1	39
Fell over	1	0	0	0	4	0	0	0	4
Starved	1	0	0	0	0	3	0	0	3
Abandoned	1	0	0	0	0	0	3	0	3
Censored[d]	3			5				6	11
Total	44	67	8	58	5	3	3	8	152

[a] Left nest during or <6 min following depredation of nest mates.
[b] ≥1 nestling fledged normally.
[c] Includes 3 nestlings that fledged <1 min after researcher visit and 2 nestlings from 1 nest that left prematurely for unknown reasons.
[d] Camera system failed (n = 2) or removed (n = 1) before predicted fledge date.

ter eliminating this group, we found no evidence of other interactions (χ^2_1 = 0.06–3.03, P = 0.22–0.97), and detected no camera effect on either survival (χ^2_1 = 0.30, P = 0.58) or predation rates (χ^2_1 = 0.95, P = 0.33). However, there appeared to be a tendency for predation rates to be lower on camera nests than non-camera nests (Fig. 1).

For camera nests, effects of nest type on initial-predation rate differed between night and day (χ^2_1 = 4.88, P = 0.027). Open nests were more vulnerable than covered nests during the day (χ^2_1 = 5.93, P = 0.015), but there was no difference at night (χ^2_1 = 0.51, P = 0.47; Table 5). We found no evidence of an interaction between time of initial predation and nest height (χ^2_1 = 2.14, P = 0.14), or between time of initial predation and nest stage (χ^2_1 = 0.10, P = 0.75). Sample sizes were too small to reliably test for interactions among nest characteristics within day and night.

Initial-predation rate increased with nestling age for days 0–8 (r_s = 0.63, P = 0.070). No relation was found, however, between daily nest survival rate (measured when the last nestling was lost) and nestling age (r_s = −0.32, P = 0.41).

Predator Identification and Behavior

We videotaped ≥11 species removing or destroying eggs or nestlings at 29 nests of 10 passerine species. Predators were identified to species at 21 nests and genus at 3 nests (Table 6; sample images in Fig. 2). At 2 nests, we narrowed predator identity to 2 species or genera. Predators at 3 nests never came into camera view, and thus, were classified as unknown. Large predators (deer, canids) were difficult to identify because only parts of their heads were in view. Wider-angle lenses used in some cameras were meant to reduce this problem, but image quality decreased as field of view increased. Images produced during the day were sharper than those produced at night with infrared light, although shadows produced by bright sunlight sometimes made daytime images difficult to interpret.

All 4 avian predations of camera nests occurred during daylight; the 22 mammalian predations were scattered throughout the 24-hr period. Only mice were documented depredating nests both day and night. At 6 nests, eggs or nestlings were depredated during >1 day or night (22–116 hr). In all these cases the pred-

Table 4. Two daily survival rate estimates[a], with 95% confidence intervals, for grassland passerine nests monitored with cameras in Stutsman and Barnes Counties, North Dakota, 1996–97.

Nest stage	Method	Survival rate	
		Daily	95% CI
Incubation	Simulated Mayfield	0.9139	0.8601–0.9677
	Mayfield	0.9320	0.8834–0.9806
Nestling	Simulated Mayfield	0.9417	0.9131–0.9704
	Mayfield	0.9431	0.9160–0.9702

[a] Simulated Mayfield estimates were calculated using nest fates based on sign at nests and exposure days based on simulated nest visits. Mayfield estimates were calculated using actual nest fates and exposure days determined from videotapes.

ators were small: mouse (1 nest), thirteen-lined ground squirrel (3), Franklin's ground squirrel (1), and brown-headed cowbird (1). At 17 nests, all nest contents were destroyed or force fledged within a single day or night. At 15 of these nests, all contents were gone in <15 min; at 2 nests (thirteen-lined ground squirrel, mouse), all contents were gone in 2–3 hr.

All predators removed 1 egg or nestling from the nest at a time, thus allowing some nestlings to escape (i.e., 8 forced fledgings at 6 nests). Forced fledgings were induced by white-tailed deer (2 nests), Franklin's ground squirrels (2), and thirteen-lined ground squirrels (2) at nests of 5 different species.

Evidence at Nests

No sign was evident at 12 of 26 depredated nests for which the final fate was documented on videotape (Table 6); 9 of the 12 nests with no sign were on the ground. Nest bowls were damaged at 6 of 12 depredated aboveground nests and only 2 of 14 depredated ground nests. Counting 2 nests that tipped over, aboveground nests accounted for 8 of 10 nest bowls that were disturbed, destroyed, or left with holes. Large mammals (badger, canid, deer) left no sign at nests they depredated. Ground squirrels varied from leaving no sign to destroying the nest bowl, and left 2–4-cm holes in 3 nests. Mice sometimes opened eggs in nests, leaving small eggshell fragments, but sometimes removed eggs from nests before opening them. Two avian predators left no sign, whereas a third completely destroyed a nest bowl and a fourth left punctured eggs.

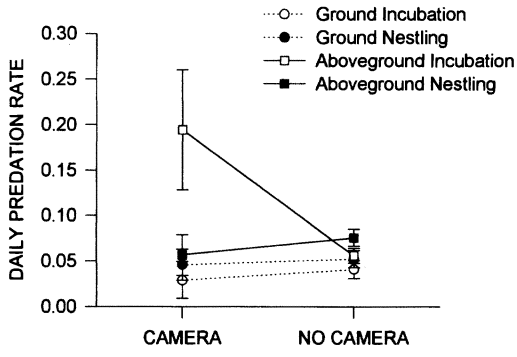

Fig. 1. Estimated daily predation rates (±1 SE) for ground and aboveground nests of grassland passerines with and without cameras, during incubation and nestling stages, in Stutsman and Barnes Counties, North Dakota, 1996–97. Numbers of nests and exposure days for each group were as follows: camera–ground–incubation 15, 68.5; camera–ground–nestling 23, 152.0; camera–aboveground–incubation 15, 36.0; camera–aboveground–nestling 17, 105.5; non-camera–ground–incubation 78, 413.5; non-camera–ground–nestling 83, 552.0; non-camera–aboveground–incubation 162, 782.5; non-camera–aboveground–nestling 138, 788.0.

Parent birds and scavengers modified evidence left by predators at some nests. A mouse killed 3 of 4 5-day-old clay-colored sparrow nestlings and left them in the nest; the parents removed the dead nestlings over the next 17 hr. Western meadowlark eggs punctured by a cowbird were scavenged by ants and beetles within 24 hr, and by a red fox within 54 hr. An adult clay-colored sparrow ate the shell and remaining contents of an egg 1 min after the mouse that had opened the egg was chased from the nest.

The length of time parent birds continued to attend depredated nests was measured for 23 camera nests. The duration of parental attendance following the last predation event was highly variable (range 0–19.6 hr) and averaged 6.8 ± 1.2 (SE) hr. The number of parental visits following the last predation also was highly variable (range 0–41) and averaged 9.7 ± 2.3. Of 15 nests last depredated during daylight, 5 were still being attended the next day; however, all 5 were deserted by 1035 hr. Of 8 nests last depredated during the night, 6 were still attended the following morning; the last of these was deserted by 1217 hr. Seven hours after predation, no nests were visited >3 times/hr.

Table 5. Diurnal and nocturnal initial-predation rates (IPR)[a] for camera-monitored grassland passerine nests in relation to stage, type, and height of nests in Stutsman and Barnes Counties, North Dakota, 1996–97.

		Diurnal predation			Nocturnal predation		
Characteristic	Exposure days	No. of depredated nests	Daily IPR	SE	No. of depredated nests	Daily IPR	SE
Nest stage							
Incubation	100	4	0.0400	0.0196	2	0.0200	0.0140
Nestling[b]	274	14	0.0511	0.0133	6	0.0219	0.0088
Nest type							
Open	187	14	0.0749[c]	0.0192	3	0.0160	0.0092
Covered	187	4	0.0214[c]	0.0106	5	0.0267	0.0118
Nest height							
Ground	211	8	0.0379	0.0131	6	0.0284	0.0114
Aboveground	163	10	0.0613	0.0188	2	0.0123	0.0086

[a] Daily predation rate censoring exposure days after the first predation event. Diurnal predation events occurred after sunrise and before sunset; nocturnal events occurred after sunset and before sunrise.
[b] Includes 3 nests with partially hatched clutches, all depredated during the day.
[c] Diurnal initial-predation rate differed between open and covered nests ($\chi^2_1 = 5.93$, $P = 0.015$). No other diurnal or nocturnal pairwise comparisons were significant ($\chi^2_1 = 0.01$–1.27, $P = 0.26$–0.91).

DISCUSSION

Predator Identification and Behavior

Nest predators identified in this study span a broad range of taxonomic groups and feeding habits. Most predators we videotaped were suspected to be predators of grassland passerine nests, although few have been documented. White-tailed deer are known to eat passerines caught in mist nests and have been suspected of nest predation (Sealy 1994), but our 2 videotaped events may be the first documentation of white-tailed deer eating nestlings. Deer mice (*Peromyscus maniculatus*) have been implicated as predators of grassland nests (e.g., Lane 1968, Rogers et al. 1997), but jumping mice (*Zapus* spp.) have not. Clutch destruction by brown-headed cowbirds (without brood parasitism) has been surmised from indirect evidence (e.g., Arcese et al. 1996) but not documented.

Although cameras proved useful for identifying predators, our predator list undoubtedly is incomplete. Striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) are common in North Dakota grasslands (Sargeant et al. 1993) and known nest predators, yet we did not videotape either species depredating a nest. Although snakes were not documented on tape, our nest searchers encountered a plains garter snake (*Thamnophis radix*) depredating Savannah sparrow nestlings. Snakes probably are easier to observe depredating nests than other species because many are diurnal and snakes swallowing prey may not leave nests quickly when humans approach.

The dynamics of predator populations over time and space increase the difficulty of completely documenting a predator community. During our study, for example, skunk and canid populations were reduced in some areas by rabies (Greenwood et al. 1997) and mange (S. H. Allen, North Dakota Game and Fish Department, personal communication), respectively. A predator list obtained with cameras also might be incomplete or biased if cameras affect the likelihood of predation by certain species. Some predators (e.g., corvids) may be attracted to novel things in their environment, and thus more likely to find camera nests than non-camera nests. In contrast, predators such as red fox and coyote are believed to be wary of novel things in their environment (Hernandez et al.

Table 6. Types of sign left by predators at 26 grassland passerine nests monitored by cameras in Stutsman and Barnes Counties, North Dakota, 1996–97.

Predator	No sign	Egg shells[a]	Nest lining disturbed	Nest bowl disturbed	Hole in nest	Nest bowl destroyed	Total nests[b]
Mouse (*Peromyscus* and *Zapus*)		2		1			2
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	3	2	4	1	1		8
Franklin's ground squirrel (*Spermophilus franklinii*)	2				2	1	5
Long-tailed weasel (*Mustela frenata*)				1			1
American badger (*Taxidea taxus*)	2						2
Red fox (*Vulpes vulpes*)		1[c]					1
Red fox or coyote (*Canis latrans*)	1						1
White-tailed deer (*Odocoileus virginianus*)	2						2
Northern harrier (*Circus cyaneus*)	1						1
Hawk (*Buteo* sp.)						1	1
Brown-headed cowbird (*Molothrus ater*)	1[d]	1[e]					2
Unknown[f]						1	1
None[g]						2	2

[a] 12 nests had eggs when depredated.
[b] A nest may have more than one type of sign. Sign was not evaluated at 1 nest that was partially depredated by a mouse and 2 that were partially depredated by unknown predators because the final fate was not taped or the final fate was not the predation event.
[c] Scavenged eggs punctured by cowbird.
[d] Three of 4 clay-colored sparrow eggs removed; no cowbird eggs laid.
[e] Punctured meadowlark eggs; no cowbird eggs laid.
[f] Removed nestlings out of camera view from back of nest.
[g] Active nests that tipped over; would have been classified as depredated using information from nest visitation only.

Fig. 2. Digitized images captured from videotapes: (A) mouse (probably *Peromyscus maniculatus*) killing 5-day-old clay-colored sparrow nestlings, (B) thirteen-lined ground squirrel killing adult female chestnut-collared longspur at the nest (ground squirrel had already removed 4 of 5 nestlings), (C) long-tailed weasel inspecting the camera after depredating common yellowthroat nest, (D) muzzle of white-tailed deer removing nestlings from savannah sparrow nest (black mark on lower mandible is diagnostic), (E) female brown-headed cowbird removing egg from unattended western meadowlark nest (cowbird destroyed entire 5-egg clutch), and (F) 2-day-old western meadowlark crawling back into nest 12 hr after it was displaced by the adult female when she flushed from the nest during the night.

1997*b*) and of human scent (MacIvor et al. 1990), and therefore may avoid camera nests. Although we documented 2 canids removing eggs from camera nests during our study, it is possible that canid predation was underrepresented in our data. In any case, populations of a given species may differ in their reaction to novel items and human scent, depending on the extent to which those populations have been persecuted by humans (Birkhead 1991:221, Götmark 1992:80) or habituated to human presence.

Sign and Nest Fates

Major disturbances at failed passerine nests (e.g., destroyed nest bowl, trampled vegetation) frequently have been attributed to predation by large mammals; empty nests with no disturbance have been attributed to predation by birds, snakes, or small mammals (Best and Stauffer 1980, Wray et al. 1982, Hoover et al. 1995, Patterson and Best 1996, Christman and Dhondt 1997). Minor disturbance and eggshell fragments in nests have been attributed to predation by small mammals, and circular holes in the bottom of nests to predation by snakes (Best 1978). These criteria were generally wrong for classifying predators of grassland passerine nests on our study areas. Variability of sign within species and overlap among species observed in our study and others (Major 1991, Brown et al. 1998, Marini and Melo 1998) indicate that evidence at nests often is unreliable for identifying predators of passerine nests.

Sign at nests also may lead to misinterpretations of nest fates. We documented cases in which successful nests appeared to have been depredated and depredated nests appeared successful. Because mistakes in assigning nest fates with sign were made in both directions, they were not reflected in overall estimates of survival rates. However, the lack of large differences in our actual and simulated Mayfield survival rates does not preclude the potential for significant levels of error from nest-visit data in other studies. Studies that involve a single nest type may be more likely to exhibit a bias in the direction of errors. Our results, for example, suggest that predation is more likely to be overestimated for aboveground nests and underestimated for ground nests.

The level of error deemed acceptable depends in part on research objectives. The maximum error rate in our sample would not likely have changed the relative importance of predation as an agent of nest failure. Most studies have implicated predation as the main cause of nest failure, often by large margins (Martin 1992). Our error rate may have been large enough, however, to change results of studies that compare predation rates to assess the effects of nest and habitat characteristics (e.g., edge, block size).

Attendance by adult birds is another type of evidence researchers use to assess nest fate when visiting nests. We found that parent birds may attend nests up to 20 hr after the last predation event. Thus, it may be misleading to assume a nest is still active based solely on the presence of an attending adult.

Predation Rates and Risk Factors

Although we did not detect a statistical difference in predation rates between nests with and without cameras, the possibility that predation was slightly lower on camera nests (as suggested by Fig. 1) could not be eliminated. If true, it may indicate that some types of predators avoided camera nests. Alternatively, it may indicate that nests surviving long enough to be in the camera treatment (i.e., surviving >1 day after being found and >1 day after camera setup) had a lower likelihood of predation than other nests.

Knowing the time of predation events at camera nests allowed us to take a new approach in exploring predation risks associated with different nest characteristics (eggs–nestlings, ground–aboveground, open–covered bowl). Time of predation events rarely has been documented in the past. Picman and Schriml (1994) documented times that predators were photographed at artificial nests and Nolan (1978:413) separated night and day predation by inspecting prairie warbler (*Dendroica discolor*) nests at least twice a day. They speculated that the relative importance of diurnal and nocturnal predation depended on the composition of the predator community. This was supported by our study, in which the preponderance of ground squirrel predation resulted in a higher proportion of daytime predations.

Some researchers have detected no difference in predation rates between incubation and nestling stages of passerines (Zimmerman 1984, Suárez and Manrique 1992, Cresswell 1997, Roper and Goldstein 1997); others have reported higher predation rates during incubation (Dixon 1978, Best and Stauffer 1980, Martin 1992) or during the nestling stage (Young 1963, Schaub et al. 1992, Suárez and Manrique 1992, Morton et al. 1993, O'Grady et al. 1996). Higher predation rates on nestlings might result from increased parental activity or begging calls of young (Cresswell 1997, Roper and Goldstein 1997). Because most activity at nests ceases at night, any increased vulnerability to predation resulting from activity levels should occur during the day (Roper and Goldstein 1997). Although small sample size limited our ability to

test this conclusively, our comparisons of diurnal and nocturnal initial-predation rates illustrate a potentially important investigative approach made possible by camera data.

Beginning with Mayfield (1961), many researchers have calculated daily nest survival separately for incubation and nestling stages, acknowledging the potential for these to have different predation rates. Most researchers are unable to test the assumption that predation rates are constant within each of these stages. If this assumption is incorrect, nest survival estimates based on exposure days may be biased (Klett and Johnson 1982). Given that nest contents and parental activity change little through incubation (Mayfield 1961, Roper and Goldstein 1997), one might expect predation rates to be relatively constant during this period (but see Willis 1973, Klett and Johnson 1982). In contrast, because of changes in nestling biomass and activity, and in parents' nest visitation rate, one might expect predation rates to increase through the nestling period (Young 1963). Data from our camera nests support this expectation; initial-predation rate increased with nestling age.

Initial-predation rate provides a better measure of predation risk relative to nest stage or nestling age than does daily survival rate. Daily survival rate includes sources of nest loss other than predation and is associated with the age of nestlings at the time the last nestling is lost rather than when the first nestling is lost. The loss of the first nestling (initial predation) more likely coincides with a predator's discovery of the nest.

The relation between predation rate and nest height has long interested researchers (e.g., Martin 1993), but few grassland nest studies have examined it. Knapton (1978) found that clay-colored sparrow nests with bases ≤10 cm from the ground were more successful than those built higher in vegetation. Aboveground nests may be more vulnerable to predation if they are more conspicuous than ground nests. If so, the risk should be greatest during the day. This prediction was not supported by our sample of camera nests, but more data are needed to test this hypothesis conclusively.

Overall, we found that aboveground nests suffered higher mortality than ground nests, even when predation mortalities were excluded. Aboveground nests can fall apart or tip over, are more vulnerable to wind damage, and may be more visible to cowbirds. The relative importance of these and other mortality factors can be difficult to assess using only information from nest visits.

Many researchers have examined the relation between nest concealment and predation rate (Nolan 1978, Martin and Roper 1988, Martin 1992, Cresswell 1997); however, few have assessed whether differences in nest bowl structure affect concealment from predators. Studies by Møller (1989) and Wray et al. (1982) suggest that the importance of nest type and concealment depends on the composition of the predator community. Conflicting results among studies about the importance of nest concealment (Martin 1992, Götmark et al. 1995, Howlett and Stutchbury 1996) may reflect differences in predator species, activity patterns, and hunting methods. Increased vulnerability to predation resulting from differences in nest visibility should be most pronounced in daylight. Data from our camera nests support this prediction; we found that open nests had higher initial-predation rates during the day. The fact that we detected no difference in predation rates between open and covered non-camera nests suggests that the importance of nest cover may only be apparent if diurnal and nocturnal predation can be separated.

Nest Abandonment and Parental Return Rates

The risk of abandonment for camera nests may be influenced by several factors. We found that abandonment was more likely if cameras were deployed at nests during incubation than during brood rearing. However, we have deployed cameras at 4 nests during egg laying (P. J. Pietz, unpublished data) and none of these was abandoned. Many species of birds are considered more vulnerable to disturbance during earlier stages of nesting (Livezey 1980, Lanyon 1994, Martin and Gavin 1995, Hill and Gould 1997). Tolerance for disturbance early in nesting may vary considerably among species (Thompson et al. 1999), individuals, or environmental conditions.

Based on abandonment rate and return times, birds seemed to be more disturbed by cameras in 1997 than 1996. Abandonment rate was considerably lower in a subsequent study in 1998 (2–3 of 29 nests; P. J. Pietz, unpublished data). Conditions in 1997 differed from the other 2 years in that cameras were deployed earlier

in the day, study areas were more remote, and weather conditions were more stressful for nesting birds.

MANAGEMENT IMPLICATIONS

The potential for bias in predation rates based on camera data may depend on the predator community. If important predator species are attracted or deterred by cameras, predation rates could be overestimated or underestimated. Even if no camera bias exists, the relative importance assigned to various predator species may be affected if sample sizes are small or predator communities are dynamic. Further, both the predators documented and their relative importance may be affected by how cameras are spatially deployed. If cameras are clustered, they will be exposed to fewer individuals of large predator species, the same individual may depredate multiple nests, and individuals that encounter >1 camera nest might learn to associate cameras with nests.

The benefits of information obtained with cameras should be weighed against the risk of increasing abandonment rates. Risk of abandonment can be reduced by delaying camera deployment until after hatch, but at the price of missing predation events that occur during the egg stage. Some evidence suggests that abandonment risk may be reduced by deploying cameras after noon.

Despite these caveats, cameras can provide information on predator and nesting ecology that is impossible to obtain by other means. For example, knowing the identity of predators, their behavior at nests, and timing of predation events can help investigators identify nest and habitat characteristics that increase nest vulnerability.

Biologists should be discouraged from attempting to identify predators using only sign at failed nests. This common practice is probably unreliable even for coarse levels of identification (e.g., large mammals). Sign is least likely to be useful in studies of ground-nesting species because most ground nests are not damaged during predation.

Errors interpreting sign that result from alteration in sign (e.g., by parent birds, scavengers) may be reduced by visiting nests more frequently, unless visits themselves affect nest outcomes (e.g., influencing predation, inducing abandonment or premature fledging). This risk is increased by the need to approach most grassland nests closely to check contents. Because adults attended nests after predation events, we recommend that empty, attended nests be checked again on the subsequent day to assess nest fate.

Cameras provide more specific and accurate information on fate of nest contents and causes of nest failure than can be obtained from periodic visits. However, detailed information from cameras presents some challenges to conventional nest-fate terminology and classification. As this type of information accumulates, researchers may need to set standards for handling the more common events, such as forced fledging.

As illustrated above, cameras proved effective for evaluating field methods currently used to assess nest success, causes of nest failure, and predator types. Such evaluations can help researchers choose the most appropriate and cost-effective methods for obtaining the data they need. Cameras also may prove useful for evaluating effects of management and research activities on grassland nesting birds.

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LITERATURE CITED

ARCESE, P., J. N. M. SMITH, AND M. I. HATCH. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proceedings of the National Academy of Sciences 93:4608–4611.

BASORE, N. S., L. B. BEST, AND J. B. WOOLEY, JR. 1986. Bird nesting in Iowa no-tillage and tilled cropland. Journal of Wildlife Management 50:19–28.

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.

BEST, L. B. 1978. Field sparrow reproductive success and nesting ecology. Auk 95:9–22.

———, AND D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. Condor 82:149–158.

BIRKHEAD, T. 1991. The magpies. T. & A. D. Poyser, London, United Kingdom.

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.

CHRISTMAN, B. J., AND A. A. DHONDT. 1997. Nest predation in black-capped chickadees: how safe are cavity nests? Auk 114:769–773.

CRESSWELL, W. 1997. Nest predation rates and nest detectability in different stages of breeding in blackbirds *Turdus merula*. Journal of Avian Biology 28:296–302.

CUSTER, T. W. 1973. Snowy owl predation on Lapland longspur nestlings recorded on film. Auk 90:433–435.

DANIELSON, W. R., R. M. DEGRAAF, AND T. K. FULLER. 1996. An inexpensive compact automatic camera system for wildlife research. Journal of Field Ornithology 67:414–421.

DEARBORN, D. C. 1996. Video documentation of a brown-headed cowbird nestling ejecting an indigo bunting nestling from the nest. Condor 98: 645–649.

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

DIXON, C. L. 1978. Breeding biology of the Savannah sparrow on Kent Island. Auk 95:235–246.

FRANZREB, K. E., AND J. L. HANULA. 1995. Evaluation of photographic devices to determine nestling diet of the endangered red-cockaded woodpecker. Journal of Field Ornithology 66:253–259.

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

———, D. BLOMQVIST, O. C. JOHANSSON, AND J. BERGKVIST. 1995. Nest site selection: a trade-off between concealment and view of surroundings? Journal of Avian Biology 26:305–312.

GREENWOOD, R. J., W. E. NEWTON, G. L. PEARSON, AND G. J. SCHAMBER. 1997. Population and movement characteristics of radio-collared striped skunks in North Dakota during an epizootic of rabies. Journal of Wildlife Diseases 33: 226–241.

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.

HASKELL, D. G. 1995. Forest fragmentation and nest predation: are experiments with Japanese quail eggs misleading? Auk 112:767–770.

HERKERT, J. R. 1995. An analysis of midwestern breeding bird population trends: 1966–1993. American Midland Naturalist 134:41–50.

HERNANDEZ, F., D. ROLLINS, AND R. CANTU. 1997*a*. Evaluating evidence to identify ground-nest predators in west Texas. Wildlife Society Bulletin 25: 826–831.

———, ———, AND ———. 1997*b*. An evaluation of Trailmaster® camera systems for identifying ground-nest predators. Wildlife Society Bulletin 25:848–853.

HILL, D. P., AND L. K. GOULD. 1997. Chestnut-collared longspur (*Calcarius ornatus*). The birds of North America, number 288. The American Ornithologists' Union, Washington, D.C., USA, and The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

HOOVER, J. P., M. C. BRITTINGHAM, AND L. J. GOODRICH. 1995. Effects of forest patch size on nesting success of wood thrushes. Auk 112:146–155.

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

HUSSELL, D. J. T. 1974. Photographic records of predation at Lapland longspur and snow bunting nests. Canadian Field-Naturalist 88:503–506.

IGL, L. D., AND D. H. JOHNSON. 1997. Changes in breeding bird populations in North Dakota: 1967 to 1992–93. Auk 114:74–92.

INNES, J., B. CROOK, AND P. JANSEN. 1994. A time-lapse camera system for detecting predators at nests of forest birds: a trial with North Island kokako. Pages 439–448 *in* I. Bishop, editor. Proceedings of Resource Technology '94. University of Melbourne, Melbourne, Australia.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

JOHNSON, R. G., AND S. A. TEMPLE. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management 54:106–111.

KLETT, A. T., AND D. H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. Auk 99:77–87.

KNAPTON, R. W. 1978. Breeding ecology of the clay-colored sparrow. Living Bird 17:137–158.

KNOPF, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247–257.

KRISTAN, D. M., R. T. GOLIGHTLY, JR., AND S. M. TOMKIEWICZ, JR. 1996. A solar-powered transmitting video camera for monitoring raptor nests. Wildlife Society Bulletin 24:284–290.

LANE, J. 1968. Baird's sparrow. Pages 745–765 *in* A. C. Bent, editor. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. National Museum Bulletin 237, part 2. Smithsonian Institution Press, Washington, D.C., USA.

LANYON, W. E. 1994. Western meadowlark (*Sturnella*

neglecta). The birds of North America, number 104. The American Ornithologists' Union, Washington, D.C., USA, and The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

LIVEZEY, B. C. 1980. Effects of selected observer-related factors on fates of duck nests. Wildlife Society Bulletin 8:123–128.

LOKEMOEN, J. T., AND R. R. KOFORD. 1996. Using candlers to determine the incubation stage of passerine eggs. Journal of Field Ornithology 67: 660–668.

MACIVOR, L. H., S. M. MELVIN, AND C. R. GRIFFIN. 1990. Effects of research activity of piping plover nest predation. Journal of Wildlife Management 54:443–447.

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

———, AND G. GOWING. 1994. An inexpensive photographic technique for identifying nest predators at active nests of birds. Wildlife Research 21:657–666.

———, 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. 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, S. G., AND T. A. GAVIN. 1995. Bobolink (*Dolichonyx oryzivorus*). The birds of North America, number 176. The American Ornithologists' Union, Washington, D.C., USA, and The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

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

———. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 *in* J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

———. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897–913.

———, AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51–57.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

———. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MILLER, C. K., AND R. L. KNIGHT. 1993. Does predator assemblage affect reproductive success in songbirds? Condor 95:712–715.

MØLLER, A. P. 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos 56:240–246.

MOORS, P. J. 1983. Predation by mustelids and rodents on the eggs and chicks of native and introduced birds in Kowhai Bush, New Zealand. Ibis 125:137–154.

MORTON, M. L., K. W. SOCKMAN, AND L. E. PETERSON. 1993. Nest predation in the mountain white-crowned sparrow. Condor 95:72–82.

NOLAN, V. JR. 1978. The ecology and behavior of the prairie warbler *Dendroica discolor*. Ornithological Monographs No. 26.

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.

OUCHLEY, K., R. B. HAMILTON, AND S. WILSON. 1994. Nest monitoring using a micro-video camera. Journal of Field Ornithology 65:410–412.

PATTERSON, M. P., AND L. B. BEST. 1996. Bird abundance and nesting success in Iowa CRP fields: the importance of vegetation structure and composition. American Midland Naturalist 135:153–167.

PETERJOHN, B. G., AND J. R. SAUER. 1993. North American breeding bird survey annual summary 1990–1991. Bird Populations 1:52–67.

PETTINGILL, O. S., JR. 1976. Observed acts of predation on birds in northern lower Michigan. Living Bird 15:33–41.

PICMAN, J. 1987. An inexpensive camera setup for the study of egg predation at artificial nests. Journal of Field Ornithology 58:372–382.

———, AND L. M. SCHRIML. 1994. A camera study of temporal patterns of nest predation in different habitats. Wilson Bulletin 106:456–465.

POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

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.

ROGERS, C. M., M. J. TAITT, J. N. M. SMITH, AND G. JONGEJAN. 1997. Nest predation and cowbird parasitism create a demographic sink in wetland-breeding song sparrows. Condor 99:622–633.

ROPER, J. J., AND R. R. GOLDSTEIN. 1997. A test of the Skutch hypothesis: does activity at nests increase nest predation risk? Journal of Avian Biology 28:111–116.

SARGEANT, A. B., R. J. GREENWOOD, M. A. SOVADA, AND T. L. SHAFFER. 1993. Distribution and abundance of predators that affect duck production–prairie pothole region. U.S. Fish and Wildlife Service Resource Publication 194.

SAVIDGE, J. A., AND T. F. SEIBERT. 1988. An infrared trigger and camera to identify predators at artificial nests. Journal of Wildlife Management 52: 291–294.

SAUER, J. R., AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 53:137–142.

SCHAUB, R., R. L. MUMME, G. E. WOOLFENDEN. 1992. Predation on the eggs and nestlings of Florida scrub jays. Auk 109:585–593.

SEALY, S. G. 1994. Observed acts of egg destruction, egg removal, and predation on nests of passerine

birds at Delta Marsh, Manitoba. Canadian Field-Naturalist 108:41–51.

SLOAN, S. S., R. T. HOLMES, AND T. W. SHERRY. 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. Journal of Wildlife Management 62: 529–539.

SUÁREZ, F., AND J. MANRIQUE. 1992. Low breeding success in Mediterranean shrubsteppe passerines: Thekla lark *Galerida theklae,* lesser short-toed lark *Calandrella rufescens,* and black-eared wheatear *Oenanthe hispanica.* Ornis Scandinavica 23:24–28.

SYKES, P. W., JR., W. E. RYMAN, C. B. KEPLER, AND J. W. HARDY. 1995. A 24-hour remote surveillance system for terrestrial wildlife studies. Journal of Field Ornithology 66:199–211.

THOMPSON, F. R., III, W. DIJAK, AND D. E. BURHANS. 1999. Video identification of predators at songbird nests in old fields. Auk 116:259–264.

VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288.

WILLIS, E. O. 1973. Survival rates for visited and unvisited nest of bicolored antbirds. Auk 90:263–267.

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.

WRAY, T., II, K. A. STRAIT, AND R. C. WHITMORE. 1982. Reproductive success of grassland sparrows on a reclaimed surface mine in West Virginia. Auk 99:157–164.

YOUNG, H. 1963. Age-specific mortality in the eggs and nestlings of blackbirds. Auk 80:145–155.

ZIMMERMAN, J. L. 1984. Nest predation and its relationship to habitat and nest density in dickcissels. Condor 86:68–72.

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SELECTION OF DAY ROOSTS BY RED BATS IN MIXED MESOPHYTIC FORESTS

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Abstract: Limited information exists on the choice of day roosts by red bats (*Lasiurus borealis*) in mature deciduous forests. We radiotracked 10 adult female and 4 adult male red bats as they used 44 day roosts in mixed mesophytic forests in eastern Kentucky during May through August 1996–97. On average ($\bar{x} \pm$ SE), bats roosted 16.5 ± 0.3 m above ground in the outer foliage of the canopy of 13 different species of hardwood trees; no conifer or snag was used as a day roost. Roost trees were dominant and codominant trees averaging 40.8 ± 1.9 cm dbh. Most roost trees (77.3%) were on ridge tops of upland forests. Each bat used an average of 3.1 roost trees and switched roost trees every 2.3 days in an area <40 m^2. Day roosts were 277 ± 30 m from forest edge, with no roost located <50 m from any edge. These data indicate that choice of day roosts by red bats inhabiting tracts of mature contiguous forest differs from those in fragmented habitats.

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Key words: bats, day roost, *Lasiurus borealis,* mixed mesophytic forest, radiotelemetry, red bat.

The richness of Nearctic bat species has been correlated with the presence or absence of roosting sites (Humphrey 1975), and most bat conservation efforts focus on the protection of roosting sites and surrounding habitat. This strategy can be effective for species of bats that occupy roosts that are predictable in time and space (i.e., caves, man-made structures, etc.), but is less adequate for bats that select ephemeral roosts such as snags and live trees (Fenton 1997). Roost lability is an inherent problem for bats that use ephemeral roosts (Kunz 1982), and these species of bats frequently switch roosts to decrease commuting costs to foraging areas, choose alternate microclimates, reduce predation and lower ectoparasite exposure (Lewis 1995). Therefore, it may be necessary to protect large parcels of forest possessing structural heterogeneity to adequately conserve habitat for many forest-roosting bat species (Brigham et al. 1997, Kalcounis and Brigham 1998, Ormsbee and McComb 1998, Rabe et al. 1998).

Factors important to the selection of roosting

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