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Identification of Sprague's Pipit Nest Predators

Stephen K. Davis, Stephanie L. Jones, Kimberly M. Dohms, and Teslin G. Holmes

Abstract. Nest predation is the primary factor influencing grassland songbird reproductive success. Understanding factors driving spatial and temporal variation in nest survival requires that we identify the primary nest predators and factors influencing predator abundance and behavior. Predation events are rarely witnessed, and the identification of nest predators is inferred, often incorrectly, from nest remains or observations of potential predators. We used video photography to identify predators of Sprague's Pipit (Anthus spragueii) nests in Saskatchewan and Montana. We monitored 60 nests in Saskatchewan and 11 nests in Montana and documented at least ten different species preying upon eggs and nestlings. Northern Harrier (Circus cyaneus) and thirteenlined ground squirrel (Ictidomys tridecemlineatus) were the most common nest predators documented on videotape, along with mouse (Peromyscus spp.), vole (Microtus spp.), deer (Odocoileus spp.), striped skunk (Mephitis mephitis), coyote (Canis latrans), Black-billed Magpie (Pica hudsonia), Western Meadowlark (Sturnella neglecta), and gartersnake (Thamnophis spp.). Most predation events occurred during the nestling stage and primarily during the day, potentially due to the increased activity of adults feeding young and of the nestlings begging for food. The diverse predator communities documented destroying grassland songbird nests presents many challenges for land managers attempting to increase reproductive success of Sprague's Pipits and other priority grassland birds.

Key Words: grassland birds, nest predation, nest predators, Northern Harrier, Sprague's Pipit, thirteen-lined ground squirrel, video monitoring, Western Meadowlark.

rassland species experience higher rates of nest predation than birds nesting in forest and wetland habitats (Martin 1993). Although nest success can be highly variable, some studies show predation rates for grassland songbird nests to be as high as 50–70% (Winter 1999, Davis and Sealy 2000). Predation is often the primary cause of nest failure (Davis 2003, Jones et al. 2010). Understanding factors driving spatial and temporal variation in nest survival requires that we identify nest predators and factors influencing predator abundance and

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behavior. Such information may allow land managers to prescribe appropriate land use and management regimes that are beneficial to grassland nesting birds (Phillips et al. 2003, Thompson and Ribic, chapter 2, this volume).

Predation events are rarely witnessed and identification of nest predators is inferred, often incorrectly, from nest remains or observations of potential predators (Larivière 1999, Pietz and Granfors 2000a, Williams and Wood 2002). Identification of nest predators has previously relied on artificial nests (Davison and Bollinger 2000). Although these experiments allow researchers to acquire large sample sizes and possibly identify predator guilds (e.g., avian, small mammal, mid-sized mammal), species identification is difficult and there are potential biases associated with artificial nests (Major and Kendal 1996, Thompson and Burhans 2004). Video monitoring has become an important method of studying nesting behavior and provides a reliable means of identifying nest predators and accurately assessing nest fate (Pietz and Granfors 2000a, Sanders and Maloney 2002, Renfrew and Ribic 2003). Unlike opportunistic field observations, video monitoring is not biased by time of day or detectability of predators.

We used video photography to identify predators of Sprague's Pipit (Anthus spragueii) nests in Saskatchewan and Montana. Sprague's Pipit (hereafter pipit) is a ground-nesting passerine of the northern mixed-grass prairie. Pipit populations have declined dramatically (Sauer et al. 2008), and the species is listed as threatened in Canada (COSEWIC 2000) and has been recommended for listing in the United States (USFWS 2010). Like most grassland passerines, reproductive success appears to be influenced primarily by nest predation (Davis and Sealy 2000, Davis 2003, Jones and Dieni 2007, Jones et al. 2010). Davis and Fisher (2009) witnessed thirteen-lined ground squirrel (Ictidomys tridecemlineatus) and Northern Harrier (Circus cyaneus) predation on radio-tagged pipit nestlings and fledged juveniles, but it is unknown to what extent these species are important nest predators. Our objectives were to (1) determine which animals prey upon Sprague's Pipit eggs and young, (2) determine the extent to which pipit nest predator communities overlap in two geographic regions, and (3) describe the behaviors of pipits and nest predators to assist researchers interested in monitoring pipit reproductive success and determining nest fate.

METHODS

Study Site

Fieldwork was conducted at the north end of Last Mountain Lake in south-central Saskatchewan, Canada (51°48'N, 107°57'W), during 2005-2008 and Bowdoin National Wildlife Refuge (NWR) in north-central Montana, U.S. (48°24'N, 107°39'W), during 2002-2007. Study sites consisted of four native mixed-grass prairie pastures and four planted hay fields in Saskatchewan and four native mixed-grass prairie sites in Montana. Detailed site descriptions are provided in Davis (2009) and Davis and Fisher (2009) for Saskatchewan sites and Jones and Dieni (2007) and Jones et al. (2010) for Montana sites. Saskatchewan pastures were grazed lightly by cattle throughout the breeding season, and having did not occur until early August. Bowdoin NWR has not been grazed by cattle for \geq 26 years, and prescribed spring burning occurred on a different site in each of 2000, 2004, and 2007.

Nest Searching and Monitoring

We conducted fieldwork between May and August, primarily from 06:00 to 14:00 Mountain Daylight Time (MDT) in Saskatchewan and throughout the day in Montana. Nest searches were conducted by systematically dragging a 25-m nylon rope weighted with aluminum and tin cans through fields to flush incubating birds off nests (Davis 2003). We also located nests using behavioral observations and fortuitously while conducting other activities on the sites. We recorded the location of each nest with a hand-held Global Positioning System unit and marked nests with colored surveyor flags 5 m south and north of the nest (Saskatchewan) and with a strip of plastic flagging on the ground approximately 2.5 m on either side of the nest (Montana).

Camera Monitoring

In Saskatchewan, we installed small (37 mm \times 86 mm) color, infrared video cameras (National Electronics Bullet C/IR Low Light Color Bullet Camera, Brookvale, NSW, AU) mounted on small metal stands (70 mm) at randomly selected pipit nests. We installed cameras during early to mid-incubation (two at day 3 and one at day 6) and during the nestling stage (one each at day 3 and

day 7) in 2004 and 2005 as part of a pilot project. In 2006 and 2007, we installed cameras at nests from mid- to late incubation (8.7 \pm 3.1SD days; n = 32) or shortly after hatching (2.3 \pm 1.7 days; n = 7) as part of a nestling provisioning study (Dohms 2009). Cameras were removed from the nesting area when the young fledged the nest or the nest failed. In 2008, we installed cameras during early incubation as part of an incubation attentiveness study (4.7 \pm 1.5SD days; n = 16; Donald 2009) and videotaped nests until hatching or the nest failed. We covered each camera with local vegetation, and set cameras 30-50 cm from the nest entrance to minimize disturbance. Cameras were connected via coaxial cable (RG6) to a time-lapse 24-hr videocassette recorder (VCR, Sanyo SRT 2400DC or 4040DC, Concord, ON) and 12-V, deep-cycle marine battery located at least 50 m from the nest and concealed beneath a vented box. The VCR time-lapse feature allowed 24 hr of activity to be recorded on 8-hr videotapes at about 4-5 images/sec. We changed videotapes every 24 hr and batteries every 48 hr or when they had discharged. Cameras recorded nests regardless of weather conditions, but we did not install cameras when it was raining or when temperatures were <5°C to minimize impacts on nesting females, eggs, or young. We checked nests using a hand-held color video monitor when changing videocassettes and every 2-3 days as part of the regular nest-monitoring schedule.

In Montana, we used the miniature video camera systems described in Pietz and Granfors (1998) on four nest monitoring sites (Jones et al. 2010). Methodologies were similar to those used in Saskatchewan except that cameras were deployed at nests as early in the incubation period as possible and where surrounding vegetation was high enough to conceal the camera.

We used the logistic exposure method (Shaffer 2004) to estimate daily nest survival for nests with and without cameras and for video-monitored nests in the incubation and nestling stages. We considered two separate models, each with only the categorical covariates of interest (camera vs. non-camera and incubation vs. nestling stage). For the camera nest comparison, we also restricted our analysis to nests that were >6 days into incubation because most of our camera nests were monitored after the sixth day of incubation (see below). We conducted analyses only for nests in Saskatchewan because of the small sample of

video-monitored nests in Montana. We estimated cause-specific daily rates of predation, abandonment, and failures due to other causes using a multinomial logistic regression and an interceptonly model; this model estimates an intercept for each class of failure, which represents the daily probability of failure to that cause. For losses to more specific causes and specific predators, we simply report the frequency of events because the number of events was too small for more rigorous model-based approaches.

RESULTS

Saskatchewan

We monitored 60 nests with cameras in Saskatchewan; 20 nests successfully fledged at least one host young, three nests were abandoned (two nests within two days and one nest >1 week after setting up the camera), eight nests failed due either to extended periods of cool, wet weather (n = 5), Brown-headed Cowbird (Molothrus ater) parasitism (n = 1), or infertile eggs (one female incubated for at least 21 days before abandoning the clutch), and one nest was buried by a northern pocket gopher (Thomomys talpoides). The fate of one nest could not be determined because vegetation blocked the camera during the latter part of the nesting period. A total of 27 nests used for video monitoring were predated, with 17 predation events captured on video. Five nests were depredated after the camera system was removed, and the remainder failed to document predators because of technical problems (e.g., dead batteries or faulty equipment) and cattle knocking over one of the cameras. At least seven species were recorded preying upon pipit nests (Table 14.1). Four nests were preyed upon during the incubation period and the remainder (n = 13) during the nestling period. The number of days that nests were monitored by cameras during the incubation period was greater than the nestling period (370 vs. 303 exposure days). However, 89% of incubation exposure days occurred after the sixth day of incubation. Predation events occurred throughout the 24-hr time period, but were most prevalent during daylight hours (Table 14.2).

Small mammals were the most common predator of pipit nests in Saskatchewan (Table 14.1). A vole (*Microtus* spp.) mutilated five 1-day-old nestlings, but it was not clear if the young were alive at the time since the female had been absent from

TABLE 14.1

	Saskatch	Montana			
Predator	Incubation	Nestling	Nestling		
Thirteen-lined ground squirrel (Ictidomys tridecemlineatus)	1	5			
Vole (<i>Microtus</i> spp.)		1			
Mouse (Peromyscus spp.)			1		
Deer (Odocoileus spp.)	2	. 2			
Striped skunk (Mephitis mephitis)		1			
Coyote (Canis latrans)	1				
Northern Harrier (Circus cyaneus)		2	3		
Black-billed Magpie (Pica hudsonia)		2			
Western Meadowlark (Sturnella neglecta)			2		
Gartersnake (Thamnophis spp.)			1		

Predators recorded on video preying upon Sprague's Pipit nests during the incubation and nestling stages in Saskatchewan (2005–2008) and Montana (2002–2007).

the nest for nearly 8 hr and was never recorded thereafter. Thirteen-lined ground squirrels were responsible for six of 17 predation events, making it the most common predator recorded on video; five of these events occurred during the nestling stage (Table 14.1). The single egg-predation event occurred in the evening (Table 14.2) and involved a ground squirrel consuming all four eggs (contents and shells) outside the nest in a 3-min period. The adult pipit returned to the nest 3 min later and removed the remaining egg shells, entering and departing the nest for 39 min before abandoning.

Behavior of ground squirrels depredating nestlings varied. In two of five cases the ground squirrel removed a single young; both nestlings were 5-6 days old. In one of these cases a striped skunk (Mephitis mephitis) ate the remaining three young two days later (Table 14.2). In the other three cases, multiple young were preyed upon. At one nest, 42 min elapsed between leaving with the first young and retrieving a second young. A ground squirrel visited this nest the following morning and removed the third of five nestlings (Table 14.2). At another nest, a ground squirrel removed a nestling during the late morning and again around noon the following day. The next day, a ground squirrel arrived in mid-afternoon and removed the remaining three young from this nest over a 20-min period. The last ground squirrel predation event involved the killing (chewing) of at least three of

five young in one visit. The predator removed one young from the nest at the end of the first visit then returned 17 min later and removed a headless body from the nest. Six min later the adult pipit began to remove two dead nestlings and a decapitated head from the nest. The predator returned 2.5 hr later to take the remaining nestling. At three nests, a ground squirrel was attacked by an adult pipit, but eventually managed to remove at least one young from the view of the camera. In all cases of partial predation, adults continued to feed remaining nestlings. Before abandoning their nests after complete depredations, adults continued to return to empty nests for a period of 12 min to 6 hr 12 min after the last ground squirrel visit. Nestling ages at the time of ground squirrel predation ranged from shortly after hatch to fledging age (12 days), with most nestlings being five days or older (Table 14.2).

All other predators documented on video consumed the entire nest contents. Deer (*Odocoileus* spp.) consumed two clutches of eggs in <20 sec and two nests with nestlings in <53 sec, and a coyote (*Canis latrans*) consumed eggs in 22 sec. Black-billed Magpies (*Pica hudsonia*) made multiple visits to the same nests over a 9–12-min period, and Northern Harriers removed five nestlings over a 3 hr 32 min period at one nest and four nestlings in a 4-min period at a second nest.

Daily nest survival rates were similar between the incubation (0.982; 95% CI = 0.969-0.989) and

Snake			Avian			Small mammal			Mid-large sized mammal					
Arrival time	Depart (sec)	Age (days)	Arrival time	Depart (sec)	Species	Age (days)	Arrival time	Depart (sec)	Species	Age (days)	Arrival time	Depart (sec)	Species	Age (days
20:11	60	13	07:45	210	BBMA	11	12:54	367	13-lined ^{C1}	7	00:53	3	Skunk ^{E3}	7
			09:10	_	BBMA	2	08:02	0	13-lined ^{C2}	8	03:43	4	Coyote	5*
			16:02	677	NOHA	10	10:41	167	13-lined ^{D1}	6	04:08	· 6	Deer	12
			13:59	266	NOHA	12	11:53	61	13-lined ^{D2}	7	23:42	49	Deer	2
			21:08	360	NOHA	7	15:44	411	13-lined ^{D3}	8	20:46	67	Deer	11*
			17:28	22	NOHA	7	09:29	446	13-lined	11	00:56	19	Deer	11*
			11:43	866	NOHA	4	10:32	1,380	13-lined	1				
			20:43	420	WEME ^{A1}	9	15:43	523	13-lined ^{E1}	5				
			06:14	24	WEME ^{A2}	10	18:54	417	13-lined	8*				
			19:04	613	WEME ^{B1}	8	00:39	7,487	Mouse	10				
			07:49	904	WEME ^{B2}	9	22:38	28,258	Vole	1				

 TABLE 14.2

 Time of day (MDT) predators appeared in view of the camera (Arrival Time), age in days of eggs or nestlings at time of predation (Age), and amount of time passed

 between attending adult departure from the nest and arrival of nest predators (Depart) in Saskatchewan (2005–2008) and Montana (2002–2007).

NOTES: Superscripts sharing the same letter but with different numbers indicate the same nest predated on different days. Species include Black-billed Magpie (BBMA), Northern Harrier (NOHA), Western Meadowlark (WEME), thirteen-lined ground squirrel (13-lined), and striped skunk (Skunk). Asterisk indicates incubation day; all other predation events occurred during the nestling period.

nestling stages (0.964; 95% CI = 0.946–0.977) of video-monitored nests. Furthermore, nest survival was similar between camera (0.855; 95% CI = 0.803–0.849) and noncamera nests (0.844; 95% CI = 0.813–0.871), even when restricting the comparison to nests that were older than the sixth day of incubation (0.845; 95% CI = 0.789–0.887 vs. 0.849; 95% CI = 0.815–0.877, respectively). We estimated cause-specific failure rates based on 674 camera observation days, 22 predation events, 3 abandonments, and 8 losses to other causes. The daily probability of loss to predation (0.033; 95% CI = 0.021–0.049) was greater than losses to abandonment (0.005; 95% CI = 0.001–0.012) and other causes (0.012; 95% CI = 0.005–0.022).

Montana

We monitored 11 pipit nests with cameras in Montana and documented seven nests being preyed upon by four species (Table 14.1). All predation events involved nestlings and occurred during daylight hours, except for the mouse predation, which occurred during the night (Table 14.2). Overall, nestlings were estimated to be 7–10 days old when they were taken from the nest.

Northern Harriers were responsible for three of seven depredated nests; the harriers consumed all the nestlings at each nest. At two nests, a harrier consumed all four nestlings over a 5-min period. At the third nest, a harrier consumed three of the nestlings on the first visit and 1 min later revisited the nest and consumed the fourth nestling. In the first nest (above), the nest was empty by 21:19 yet adult pipits continued to bring food until 22:02 and again at 06:04 the following morning; no further visits by adult pipits were recorded at the nest. In the second case, adult pipits continued to bring food to the empty nest and periodically "brood" for at least 3 hr before the camera stopped recording. Details of continued adult attendance at the third nest could not be described because vegetation obscured the video-recording.

Western Meadowlarks (*Sturnella neglecta*) preyed upon two of seven nests. At one nest, a meadowlark removed and consumed a single nestling between 20:43 to 20:48. The meadowlark visited the nest 36 min later, removed the second nestling, and pecked at the heads of the remaining two nestlings; 3 min later the meadowlark removed a third nestling from the nest. Adult pipits visited the nest during the night, and at 06:14 the following morning

a meadowlark removed the last nestling from the nest, again pecking at its head. The meadowlark left when an adult pipit arrived with food at 06:18 and the meadowlark returned again at 07:44, followed shortly by the adult pipit carrying food. No pipit adults were observed again, but a meadowlark visited the nest at 08:02. At the second pipit nest depredated by a meadowlark, a Richardson's ground squirrel (Urocitellus richardsonii) investigated the camera (ignoring the nest) at 17:35, after which a meadowlark arrived at 19:04. The meadowlark pulled two of four nestlings from the nest, and continued to peck nestlings that were outside the nest when revisiting the nest on two occasions over a 20-min period. The meadowlark left the nest when an adult pipit arrived to feed the two nestlings remaining in the nest. The meadowlark returned at 07:34 the next morning and killed another nestling. The adult pipit arrived with food at 07:49, when the last nestling was observed alive. Pipits continued to deliver food until 08:00, when the last nestling died, presumably of injuries. Deaths of the nestlings were presumed when their movements stopped. Adults continued to deliver food for 1 hr 4 min, with no further activity for another 1 hr 20 min, when the camera stopped recording.

The mouse (*Peromyscus* spp.) predation event involved a mouse entering the nest at 00:39 and killing four of the five nestlings over a 6-min period. A mouse returned the next morning at 04:19, staying at the nest for 6.8 min. The adult pipit first brought food to the nest at 05:58 and the pipits continued to visit the nest until the last nestling died by 11:34, probably due to injuries sustained earlier.

During incubation, a gartersnake (*Thamnophis* spp.) visited a nest for 3.7 min without removing an egg. The same nest was visited 13 days later by a gartersnake entering the nest at 20:11, forcing the fledging of three 13-day-old nestlings. The gartersnake grabbed the fourth nestling by the leg and removed it from the nest at 20:14. A gartersnake returned to the nest at 22:06 and remained for 4 min. Adult pipits were recorded back at the nest at 05:00 the next morning carrying food; this behavior continued until 07:49.

DISCUSSION

Video-recording technology allowed us to identify diurnal and nocturnal predators of Sprague's Pipit nests in Saskatchewan and Montana. Until now it was unknown which species were predators of pipit nests, although mammals, snakes, and raptors were suspected (Robbins and Dale 1999). We documented at least ten different species preying upon pipit nests. Our results, combined with those reported by Davis and Fisher (2009), indicate that thirteen-lined ground squirrels and Northern Harriers are common predators of pipit nests in our study areas. Although video studies likely underestimate the number of predator species taking songbird nests due to possible avoidance of camera equipment by some species (Pietz and Granfors 2000a, Pietz at al., chapter 1, this volume), evidence is mounting that grassland songbird predator communities are diverse, and small mammals, particularly thirteen-lined ground squirrels, are common nest predators (Schaeff and Picman 1988, Pietz and Granfors 2000a, Renfrew and Ribic 2003, Ribic et al., chapter 10, this volume). Our results also support past studies showing that video-camera systems do not reduce nest survival rates of camera-monitored nests (Pietz and Granfors 2000a, Renfrew and Ribic 2003, Powell et al., chapter 5, this volume).

Our video cameras also captured other seemingly uncommon predators implicated in previous video studies such as deer, mice, and voles (Pietz and Granfors 2000b, Renfrew and Ribic 2003). All are commonly encountered in our study areas and likely take more nests than wildlife biologists realize (Pietz and Granfors 2000b), although commonly suspected species such as coyote, snake, and striped skunk were also captured on video. We documented only one canid predator in our study, despite having an active coyote den on one of our study plots in Saskatchewan. Furthermore, few canids were recorded on cameras in North Dakota (Pietz and Granfors 2000a), even though both red fox (Vulpes vulpes) and coyote are common predators of waterfowl nests (Sargeant et al. 1993). These canids may not target passerine nests as they do waterfowl nests because of the relatively low reward and low probability that a flushed passerine is associated with a nest (A. B. Sargeant, pers. comm.). Canids may also avoid camera nests because they are wary of novel things in their environment (Hernandez etal.1997) and of human scent (MacIvor et al. 1990). Furthermore, wild canids are typically "hunted" outside protected areas in our region and may avoid our study sites, particularly during the day, when human activity is the greatest. Although similar reasoning could be made for deer, unlike

canids, deer appear to be a relatively common predator of grassland songbird nests (Pietz and Granfors 2000b). The relatively large number of predation events attributed to deer may simply be a function of their abundance, or, unlike canids, they may be attracted to novel objects in their environment such as nest markers and video equipment.

We recorded two cases of predation by Western Meadowlarks in Montana, which was unexpected given our small sample size. We also recorded a meadowlark visiting a nest in Saskatchewan, but the bird simply investigated the nest area and then departed. Meadowlarks are known to prey upon eggs and young and to scavenge carcasses (Creighton and Porter 1974, Davis and Lanyon 2008). Meadowlarks killed the nestlings at two nests in our study but did not consume all individuals, even when they returned to the nest the following day. Nest predation may represent opportunistic feeding for this species or some mechanism to reduce competition from neighbors (Creighton and Porter 1974).

Our results suggest that predation risk is greatest during the day, especially during the nestling period. Approximately 72% of our recorded predation events occurred during daylight hours. The importance of nocturnal and diurnal predators likely varies according to local predator guilds. For example, Pietz and Granfors (2000a) reported that most grassland bird nests were taken by diurnal predators, whereas Renfrew and Ribic (2003) documented a greater proportion of nocturnal predation events; likely reflecting the prevalence of thirteen-lined ground squirrels and mid-sized mammals in their respective study areas. Over 83% of predation events we documented occurred during the nestling period. This may reflect less intensive video monitoring during the early incubation period in Saskatchewan, given that 94% of our sampling period occurred after the sixth day of incubation. On the other hand, our data may reflect real predation patterns. Assuming 13 days for incubation and 12 days for brood rearing (Davis 2009), 79% of video-monitored pipit nests survived the incubation period and 64% survived the nestling period. Incubation and nestling stage survival was 21% and 7%, respectively, for all 187 nests monitored in Saskatchewan (S. K. Davis, unpubl. data). Furthermore, past studies found pipit nest survival to be influenced by nest age, with nest survival being highest during the

incubation period and lowest during the nestling period (Davis 2003, Jones and Dieni 2007, Jones et al. 2010), particularly just prior to fledging (Davis et al. 2006). Davis (1994) found a similar pattern for pipits and four other grassland songbird species in Manitoba. Patterson and Best (1996) reported higher survival rates during the incubation period for four of five species breeding in Iowa. The lower survival rates during the nestling period may be due to diurnal predators cueing on the increased activity of adults feeding young and nestlings begging for food (Haskell 1994). Indeed, Dohms (2009) found that provisioning rates of pipits increased as the young aged. Furthermore, video recording revealed increased nestling activity inside and outside the nest a few days prior to fledging (S. K. Davis, unpubl. data).

Video recording also allowed us to document interesting behaviors of pipits and nest predators. We documented three cases of nest defense against thirteen-lined ground squirrel. In each case, the ground squirrel arrived when the pipit was away from the nest and the pipits attacked the squirrel upon arrival, with mixed results. In two cases the ground squirrel ran off with a single nestling, while in the third case the female pipit thwarted the ground squirrel from removing nestlings during the first attack only. The ground squirrel returned to the nest on two separate occasions and killed all the nestlings despite the attacks from the female. The male (color banded) was also observed at the nest, but we could not determine whether he assisted the female in the attacks. The frequency or success of nest defense by pipits is difficult to assess because of the limited field of view of the cameras and our review of videotapes in Saskatchewan was restricted to nests with known predation events (see also Pietz and Granfors 2005). However, nest defense by pipits appears to be a useful strategy against smaller predators, as two of the three nests successfully fledged young. This may in part explain why all but one nest predation by small mammals and western meadowlarks occurred while the adult pipits were away from the nest. In contrast to diurnal predation events, females were typically on the nest just prior to nocturnal predations and departed the nest shortly after the arrival of the predator.

Over the years, we have often noticed partial egg and nestling loss while monitoring grassland bird nests. We suspected that predators were removing eggs and nestlings between our nest visits, but had no way of confirming our suspicions. Although we could not determine whether the same individual was responsible for multiple predation events, we did confirm that the same species was responsible for partial predation events on different days. Thirteen-lined ground squirrels were observed depredating nests on two consecutive days at one nest and three consecutive days at another nest. We also documented Western Meadowlarks preying upon the same nest on two consecutive days at two different nests. Future studies might consider determining whether individuals exposed to partial nest predation alter their nest attendance behavior in an attempt to thwart future predation attempts. Our only other case of multiple visits by the same nest predator involved a gartersnake. A gartersnake visited the nest during the incubation stage but did not consume any of the eggs. A gartersnake then visited the nest prior to fledging and captured at least one nestling. Some researchers question whether snakes might delay depredating nests containing eggs until the nestlings develop, to take advantage of the increased nutrient reward (L. A. Powell, pers. comm.). Not all multiple predation events were due to one species. We documented one case of predation first by a thirteenlined ground squirrel, followed by striped skunk two days later. We could not determine whether the two events were completely independent or whether partial predation by the ground squirrel provided visual or olfactory cues for the skunk.

The diverse predator communities documented destroying grassland songbird nests present many challenges for land managers attempting to increase reproductive success of pipits and other grassland songbirds. The predator guilds documented in camera studies to date are associated with a variety of habitats, with some species associated with edge habitat (e.g., striped skunk) and others occupying interior grasslands (e.g., thirteen-lined ground squirrel) (Renfrew and Ribic 2003, Renfrew et al. 2005, Grant et al. 2006). However, further research on identification of nest predators provides an important step toward informed and effective management for grassland songbirds (Thompson and Ribic, chapter 2, this volume). Given the importance of Northern Harriers and thirteen-lined ground squirrels as predators of pipit nests in our studies, future research should examine the foraging ecology

and behavior of these species to gain an understanding of how local and landscape-level factors influence their abundance. In addition, experimental studies are needed to determine whether deer are more likely to depredate nests with cameras or nest markers, given the number of camera nests taken by these animals in Saskatchewan and North Dakota (Pietz and Granfors 2000b).

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