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Abstract

Predators may limit populations of small carnivores indirectly through exploitative competition for resources, and directly through interference competition, including predation. We evaluated direct effects of predation by large predators on small, specialist carnivores by estimating annual survival and cause-specific mortality. We used known fate models to estimate annual survival of 23 radio-collared short-tailed weasels (*Mustela erminea*) in western Oregon in 2012–2013. Further, we reviewed published and unpublished studies of radio-tracked weasels (*Mustela spp.*) in North America, to identify main predators of weasels and survival. If the study did not report survival but did report number of days tracked and cause-specific mortalities, we extrapolated an annual survival index, based on daily survival rates (Mayfield index), to facilitate comparisons between studies. Estimated mean \pm SD annual survival of short-tailed weasels in our study was 0.26 ± 0.08 , and did not vary by season or sex of the weasel. Most (80%) predation mortalities, however, occurred in winter, and were attributed to predatory birds, suspected to be barred owls (*Strix varia*). For seven North American studies, including ours, we estimated the average annual survival index for *M. erminea* and *Mustela frenata* to be 0.37 ± 0.28 . Across studies, most mortality was attributed to predation. Predators killed weasels $> 2x$ more frequently in winter when most mortality (86%) was attributed to predatory birds. Mammalian predators, in contrast, killed weasels most frequently in summer (75%). Our results support the hypothesis that predation may play an important role limiting weasel populations in North America.

Keywords: short-tailed weasel, predation, survival, competition, barred owl

Introduction

Small predators are often killed by large predators and competitors, and predation can, potentially, limit population size of small predators (Powell 1973), affecting predator-prey dynamics (Korpimäki and Norrdahl 1989a) and competition (St-Pierre et al. 2006). Predation may facilitate the co-existence of one or more small carnivore species if predation disproportionately limits the competitively superior species (St-Pierre et al. 2006, Powell and Zielinski 1983). Thus, predation by large predators on small predators probably plays an important role in vertebrate community structure by limiting the competitive advantages that small, specialist predators may exhibit when

pursuing small-bodied prey (Powell and Zielinski 1983, Jędrzejewska and Jędrzejewski 1998). Yet, long-term interactions among large and small vertebrate predators and their shared prey remain relatively understudied (King and Powell 2007, Erlinge 1983).

Broadly distributed across the northern hemisphere, weasels, the smallest and thinnest members of genus *Mustela*, exemplify the complex life history tradeoffs experienced by small predators in complex ecosystems. Weasels are solitary, specialist predators, not much larger than their prey, but highly adapted to hunt birds and small rodents, particularly voles (*Microtus* and *Myodes spp.*). Especially when active, weasels are vulnerable to large, generalist predators, particularly those that pursue some of the same prey as weasels (Korpimäki and Norrdahl 1989b, King and

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Powell 2007), including predatory birds (Powell 1982), terrestrial carnivores (St-Pierre et al. 2006), and other weasels (Gehring and Swihart 2000). Like other mustelids, weasels have large energy requirements, and must hunt vertebrate prey daily (Powell 1978, Powell 1979, Goszczyński 1986), including during cold winter months when their high surface-to-body ratio and short fur results in high thermal energy loss to the environment (Zub et al. 2009). Weasel populations are thus strongly influenced by prey; prey availability in winter and spring (initiation of breeding season and birthing of kits) is the primary determinant of reproductive success (King 1981, Erlinge 1983). Thus, weasels must balance food (prey) acquisition, thermal limitations, and exposure to predators (Erlinge 1983, Zub et al. 2011).

Predation risk likely has a fundamental influence on weasel ecology, behavior, and morphology (Powell 1978, Powell 1982). For instance, weasels can limit energy expenditures while foraging if prey is at high density and therefore located quickly, in turn reducing predation risk and thermal heat loss to the environment (Jędrzejewski et al. 1995, Zub et al. 2009). Weasels and their prey inhabit areas with dense ground cover (Yahner 1986, Zub et al. 2008), often grassy meadows and early successional forests (Simms 1979, Wilson and Carey 1996), which may provide escape cover from large predators for both weasels and prey (Koivisto et al. 2016). Behavioral choices such as activity period also likely reflect predation risk: for example, diurnally active least weasels (*Mustela nivalis*) in Poland were most commonly killed by diurnal raptors (Jędrzejewski et al. 2000). For the larger weasels (*Mustela erminea*, *Mustela frenata*), predator avoidance mechanisms such as irregular, punctuated movements (Powell 1978) and a black-tipped tail which directs a predator strike to the tail may be direct adaptations to reduce predation risk while active (Powell 1982). For *M. erminea*, home range sizes, prey and habitat selection, and perhaps predator avoidance varies by sex. Females tend to have smaller home ranges, prefer voles, and inhabit areas with high vole abundance (Hellstedt and Henttonen 2006), whereas males tend to be more general in both

habitat and prey selection (Lisgo 1999, Edwards and Forbes 2003, Linnell et al. 2017).

Weasel populations are rarely stable. Although King and Powell (2007) concluded that weasel populations are limited by prey in most cases, Powell (1973) evaluated whether predation could limit weasel populations. He used a three-part model (raptors, weasels, and *Microtus* prey), and field observations of these species by Craighead and Craighead (1956) to parameterize the model. Although necessarily simple in structure, the model indicated weasel populations were limited by predation once annual weasel mortality from predators reached 70% (inversely, survival at or below 30%). Most additional data suggesting predation could limit weasel populations has been collected anecdotally from studies of predatory bird diets (Korpimäki and Norrdahl 1989a). In Sweden, after multi-annual rodent population peaks when least weasels (*M. nivalis*) may be abundant but rodent populations declining, predatory birds were estimated to take 80% of the weasel population, presumably because weasels became prey for predatory birds when rodents were scarce (Korpimäki and Norrdahl 1989a). Similarly, in Poland, 65% of mortality of least weasels was estimated to be from predation (Jędrzejewska and Jędrzejewski 1998). Thus, although weasel populations are undoubtedly influenced by prey availability, mortality from predation could significantly constrain weasel populations under certain circumstances (Korpimäki and Norrdahl 1989b, King and Powell 2007), such as seasons or years when shared prey for weasels and their predators are scarce.

In this paper, we use a two-part approach to evaluate the potential for weasel populations in North America to be limited by predation. First, from June 2012 to April 2013, we conducted a radio-telemetry study of short-tailed weasels (*M. erminea*) in western Oregon in which we documented causes of mortality and estimated daily and annual survival. Our primary objectives were to identify predators of weasels, estimate survival, and describe activity patterns to infer vulnerability to nocturnal versus diurnal predators. Specifically, we tested two hypotheses in our field study: 1) we

predicted lower survival in winter when shared prey of weasels and large predators were expected to be at annual lows (Erlinge 1983), 2) because males must move more to cover larger home ranges, are less selective of habitat and prey, and thus could encounter large generalist predators more frequently, we predicted that males would have lower survival. Secondly, we reviewed all published field studies and unpublished theses that examined North American weasel species (*M. erminea*, *M. frenata*, *M. nivalis*). We estimated an index of annual survival for all such studies, including our field study, predicting that survival would be lower in winter. Finally, we compared those estimates of survival to Powell's (1973) model to determine whether mortality from predation likely exceeds the threshold at which weasel populations could be limited by predators.

Methods

Study Area

Our field study was conducted on the McDonald-Dunn Research Forest, 12 kilometers north of Corvallis, Benton County, Oregon. McDonald-Dunn Research Forest is owned and managed by the Department of Forestry at Oregon State University, and is located in the foothills of the Oregon Coast Ranges at the western edge of the Willamette Valley. Elevation on the study area is 100–553 m. Vegetation on the study area is dominated by young Douglas-fir (*Pseudotsuga menziesii*) plantations with patches of dense grasses and saplings (29%), and by mature even-aged Douglas-fir plantations (46%). The rest of the study area is riparian forest dominated by mixtures of bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and Oregon white ash (*Fraxinus latifolia*), oak woodlands (*Quercus garryana*), abandoned farm fields, and cultivated farm fields (Linnell 2014). The study area has moderately steep terrain intersected by numerous small streams. Precipitation averages 103 cm annually, mostly occurring as rain during winter (November–March; Western Regional Climate Center 2014). We divided the year into two seasons, based on precipitation and breeding by weasels:

winter (November–March, non-breeding) and summer (April–October, breeding).

At least six species of predatory birds commonly occurred on the study area, including red-tailed hawks (*Buteo jamaicensis*), barred owls (*Strix varia*), great horned owls (*Bubo virginianus*), kestrels (*Falco sparverius*), and accipiters (*Accipiter striatus*, *A. cooperi*). Potential mammalian predators of weasels included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), pumas (*Puma concolor*), and skunks (*Spilogale gracilis*, *Mephitis mephitis*; Verts and Carraway 1998).

Field Study

We captured weasels in modified Tomahawk #102 live traps placed at 50 m intervals along 12 transects. Because weasels are sensitive to live trapping and can damage themselves attempting to escape (Belant 1992), we modified live traps to reduce this possibility. We attached a cubby with a small entrance hole (< 5 cm) to the back of the trap, covered the cage part of the trap with a plastic cover to protect from the weather, and attached a plastic floor which reduced or eliminated play of the trap door which can cause injuries when weasels try to escape (Belant 1992). Each trap was baited with lure (Weasel Super All Call Lure, Asa Lenon) and a freshly dead lab mouse (*Mus musculus*), and included fleece bedding. Transect length varied from 200 to 400 m due to differing feature lengths and access and had 5 to 9 traps per transect (up to 60 traps at any one time). We placed traps in sites with abundant ground cover such as logging debris (Lisgo 1999), thick shrubs, or dense grass. Additional traps were opportunistically placed at obvious habitat features along roads, including logging debris and near small streams.

Upon capture, we removed weasels from traps and sedated them with isoflurane before determining their sex, age, and weight and attaching a radio collar weighing one gram (females) or two grams (males, females; Model BD-2C, Holohil Systems Ltd., Carp, Ontario, Canada). All handling methods were conducted under Oregon State University Animal Care and Use Permit 4191 and Oregon Department of Fish and Wildlife permit 109-12.

We located each weasel at least once per day. When an individual remained in the same location for more than two days we investigated the area to determine if it was alive or dead. If the radio signal indicated that the collar was stationary, we searched the area until we located it. We documented whether the body was intact (non-consumptive mortality) or had been killed and consumed (consumptive mortality). If radio-collars were found in a pellet regurgitated by a predatory bird or near large amounts of fresh whitewash where a predatory bird had roosted, we concluded that the weasel had been killed by a predatory bird. We distinguished pellets from owls from pellets from diurnal raptors based on size and appearance (Fitch et al. 1946). Barred owls and great-horned owls were distinguished primarily based on pellet size (Terry 2004, Holt and Colleen 2007). We identified vertebrate remains in pellets by comparing bones to a reference collection at Oregon State University (Forsman et al. 1984).

We estimated biweekly Kaplan-Meier survival for weasels that retained their collars for at least two consecutive biweekly periods using known-fate models in the RMark extension for program MARK (White and Burnham 1999, Laake and Rexstad 2008). Radio-collared weasels were entered into the sample after a 48-hour collar adjustment period, and were left-censored for the time period before they entered the sample. We used univariate known-fate models with the logit link function to evaluate differences between SEX (male versus female) and SEASON (winter versus summer), and a no effects null model $S(\cdot)$; we used rMark to rank models using AIC_c (Burnham and Anderson 2002) and to estimate survival (mean and 95% confidence intervals) for each model.

During May 2012–March 2014 we used remote cameras (Bushnell model 119436) to document the activity of weasels at traps and sites where radio-collared weasels were resting. Cameras were placed approximately two meters from the entrance of the trap or resting site, either directly on the ground or attached to a 1 m fencepost and angled down. Cameras were set to record 10 seconds of video each time the camera was triggered, and set to a five second delay between camera triggers. When

the same subject resides within the camera's field of view for extended periods of time, a method is needed for determining the duration of time that has to transpire before the subsequent video clip can be considered independent and useful. To address this, we estimated the number of videos falling in temporal bin widths ranging from 1 to 60 minutes at 1 minute intervals (e.g., a 45-minute temporal bin width would mean only videos that were recorded > 45 minutes apart would be included in the sample). We then graphed temporal bin width (x-axis) and number of videos (y-axis) on the same scale (i.e. 0 to 1) and selected a bin width at the point where the slope of the tangent of the curve approached -1 (Fagen and Young 1978).

We assumed that remote camera videos could be used to estimate an index of circadian rhythm at the population level. We divided camera-days into four seasons: winter (December–February), spring (March–May), summer (June–August), and fall (September–November). We divided daily activity into three periods: diurnal, nocturnal, and crepuscular. Crepuscular activity was defined as ± 1 hour of sunrise and sunset. Diurnal activity was between one hour after sunrise until one hour before sunset and nocturnal activity was one hour after sunset until one hour before sunrise. We used the sunrise/sunset times on the 15th of each month to approximate sunrise and sunset times for that month. We used chi-squared tests to compare observed and expected seasonal activity periods for three daily time periods (diurnal, crepuscular, nocturnal). We estimated the observed activity as the number of videos in each time period. We estimated expected numbers of videos as the average proportion of each daily time period occurring in a given season multiplied by the total number of videos for that season.

Literature Review of Weasel Studies

We reviewed six studies in North America in which weasels were radio-tracked for greater than 100 days, including two studies of short-tailed weasels (Samson and Raymond 1998, Lisgo 1999), three studies of long-tailed weasels (Gehring and Swihart 2000, Richter 2005, Hajduk 2008), and one study of both species (St-Pierre et al. 2006). We

TABLE 1. Results of the literature review of survival of radio-collared weasels (*Mustela erminea*, *M. frenata*) in North America. Daily survival index was calculated as $1 - (\text{number of predation events}/\text{days tracked})$. Annual survival index was calculated as the product of daily survival index for the period of one year (365 days; $(\text{daily survival index})^{365}$). Habitat is indicated by the main vegetation cover type reported in each study.

Source	Species	Season ^a	Habitat	Predation events	Days tracked	<i>n</i> (m/f)	Daily Survival Index	Predation/ <i>n</i>	Annual Survival Index
Linnell (2014)	<i>M. erminea</i>	Both	Forest	5	1463	23 (18/5)	0.9966	0.22	0.29
Lisgo (1999)	<i>M. erminea</i>	Summer	Forest	0	898	8 (4/4)	1.0000	0.00	1.00
Samson and Raymond (1998)	<i>M. erminea</i>	Summer	Forest	1	130	11 (5/6)	0.9923	0.09	0.06
St-Pierre et al. (2006)	<i>M. erminea</i>	Summer	Forest	1	407	11 (10/1)	0.9975	0.09	0.41
St-Pierre et al. (2006)	<i>M. frenata</i>	Summer	Forest	2	777	21 (14/6)	0.9974	0.10	0.39
Gehring and Swihart (2000)	<i>M. frenata</i>	Both	Agriculture	3	915	13 (7/4)	0.9967	0.23	0.30
Hajduk (2008)	<i>M. frenata</i>	Summer	Grassland	1	326	9 (7/2)	0.9969	0.11	0.33
Richter (2005)	<i>M. frenata</i>	Both	Grassland	2	392	8 (4/4)	0.9949	0.25	0.15
Totals				15	4916	99 (67/32)	0.9972	0.14	0.37

^a Summer = May–October, Winter = November–April.

excluded two studies in which long-tailed weasels were tracked for less than 100 days or where the number of weasel tracking-days was not reported (De Van 1982, Wilson and Carey 1996). We could not find any studies in which least weasels were radio-tracked.

For each study, we summarized the number of individuals that were tracked, the number of days that each individual was tracked (Table 1), and the fate of the individual, including the source of mortality (Table 2). If a study reported trapping an individual but provided no information about number of days tracked or the fate of the individual,

TABLE 2. Proximate cause of weasel predation based on the combined data from seven studies in which investigators tracked the fate of radio-collared weasels (*Mustela erminea*, *M. frenata*) in North America, including this study.

	Avian	Mustelid	Other mammal	Total
Summer ^a	2	2	4	8
Winter ^a	6	0	1	7
Total	8	2	5	15

^aSummer = May–October (tracking-days = 3846), Winter = November–April (tracking-days = 1605).

we excluded that individual from the analysis. We used the Mayfield index (Mayfield 1975, Heisey and Fuller 1985) to estimate an index of annual survival using the daily survival rate. We chose the Mayfield index because it provides a simple, repeatable representation of survival from data commonly available in telemetry studies. The Mayfield index uses a data matrix similar to Kaplan-Meier, whereby for each day tracked, and known to be alive, the animal receives a 1. To calculate the daily survival rate, we divided the number of mortalities by the total tracking-days in a study. Since no studies other than ours reported mortality of radio-tracked animals due to causes other than predation, to make our study comparable to the others in this regard, we excluded any animal from our study that died from a cause other than predation in this analysis.

We extrapolated the daily survival rate for each study to a 365-day period representing one year to create an annual survival index for each study as $(\text{daily survival rate})^{365}$ (Mayfield 1975). In addition, we categorized the season in which the majority of each study was conducted as summer (May–October), or winter (November–April). To make studies comparable, we limited analysis to

studies in which animals were located at least once per week, and we made three assumptions: 1) animals sampled using radio-telemetry represented the population (Murray 2006), 2) all animals in a study were exposed to similar mortality risk, and 3) mortality only included predation, given that no study reviewed reported any other sources of mortality. We further tested a fourth assumption, that mortality risk was constant across the year, such that an annual survival estimate could be obtained from daily estimates, by comparing the rate of predation (number of mortalities/days tracked) between summer and winter. If unreported mortalities were attributable to a cause other than predation, then we may have underestimated the survival index.

Results

Field Study in Western Oregon

We captured 33 short-tailed weasels (23 M, 10 F) 43 times during 947 trap nights in June 2012–March 2013 (4.5 captures/100 trap-nights). Twenty-three weasels (18M, 5F) retained their collars long enough to be used in our survival analysis. For all results, we refer to the mean \pm SD. The number of tracking-days for the 23 weasels was 64 ± 55 . We documented eight mortalities, of which five were due to predation. Of the five mortalities due to predators, four were attributed to predatory birds and one was attributed to a bobcat—all occurred during winter. In the three mortalities not attributed to predation, two of the three animals had lost weight since capture, possibly indicating starvation. The third non-predation mortality was suspected to be collar related. Five individuals were censored from the analysis when they removed their radio-collars. Ten individuals were censored when their radio-collars failed.

Of the four mortalities ascribed to predatory birds, all appeared to be due to owls based on pellets or fecal whitewash found at the scene. In all four cases, the weasel was entirely consumed and in two of the four cases (weasels: M17, M07), the radio-collar was consumed and found in fragments of an owl pellet, covered in digestive fluids and weasel remains. The collar of weasel M22 was unconsumed and found next to an owl pellet that

was consistent with barred owl size dimensions. The latter pellet also contained the remains of shrew (*Sorex spp.*) and pocket gopher (*Thomomys bottae*). In the fourth case, we located the blood-stained collar of weasel M21 on a mossy branch of a big-leaf maple (*Acer macrophylla*) ~ 15m above ground where a predatory bird had eaten the weasel and discarded his collar. We found no owl pellet at the latter site, but extensive whitewash under the trunk of the tree, and the short distance to the location of a confirmed owl predation (74m), led us to conclude that the predator was most likely a large owl, although we could not discount other predatory birds. The suspected bobcat mortality was located unconsumed two meters from an abandoned road on the edge of riparian and grass/shrub cover types. We suspected bobcat because of abundant evidence of bobcat in the area (e.g. scat, remote camera videos, and tracks) and because bite marks on the weasel were consistent with bobcat canine spacing. Of the five predation mortalities, three were found within an area of high use for that individual weasel (core range, Linnell 2014), one weasel did not have enough locations to estimate a core range, and one was found 233 m from the edge of his core range. For four of the five predation mortalities, collars and remains were found in or adjacent to riparian forest. Since most were killed by predatory birds, however, the final location may not have been the kill site.

The top model in the survival analysis was the null model (Table 3). Survival (mean; 95% confidence interval (95% CI), number in sample) during summer (0.54; 95% CI: 0.15–0.88, $n = 13$) was estimated to be almost three times higher than winter (0.19; 95% CI: 0.04–0.59, $n = 13$). Contrary to our prediction, mean male survival was estimated to be higher (0.38; 95% CI: 0.14–0.71, $n = 18$) than females (0.16; 95% CI: 0.01–0.80, $n = 5$). For both SEASON and SEX, however, confidence intervals were wide and overlapped extensively. Biweekly survival based on the null model was estimated as 0.95 ± 0.08 and the cumulative estimate of survival for the 40-week period was 0.33 (95% CI = 0.13–0.63). Point estimates of survival suggested a marked decrease in December and January (Figure 1). Estimated annual survival

TABLE 3. Model selection results from the analysis of survival of radio-collared short-tailed weasels on the McDonald-Dunn study area, Benton County, OR, June 2012–March 2013. The best model is listed first with other models listed by increasing AIC_c values. Models with $\Delta AIC_c < 2.0$ were considered competitive with the best model.

Model structure ^a	K ^b	AIC _c	ΔAIC_c	W _i ^c	Deviance
S(.)	1	48.19	0	0.45	25.54
S(SEASON)	2	48.74	0.56	0.34	24.00
S(SEX)	2	49.75	1.57	0.21	25.00

^aCovariates indicate model structure SEX and SEASON; S(.), the null model, indicates no-effects of sex or season on survival.

^bNumber of parameters in model.

^cModel weight

based on the average biweekly survival rate was 0.26 (95% CI = 0.11–0.42).

We recorded 512 videos of *M. erminea* in 2716 camera-days (679 ± 51 days per season). Slope of the tangent at the two-minute bin width approached -1 and we excluded videos recorded < 2 minutes apart ($n = 72$, Figure 2). Activity periods appeared to shift with seasons (Figure 3). Weasels were primarily diurnal in summer ($\chi^2 = 15.6, P < 0.001$) when they were most active ($n = 237$ detections), crepuscular in fall ($\chi^2 = 7.5, P = 0.02, n = 63$) and spring ($\chi^2 = 3.6, P = 0.16, n = 81$), and followed no obvious pattern (arrhythmic) in winter ($\chi^2 = 0.1, P = 0.97, n = 59$). Weasels were, however, more nocturnally active in the winter than in any other season (Figure 3).

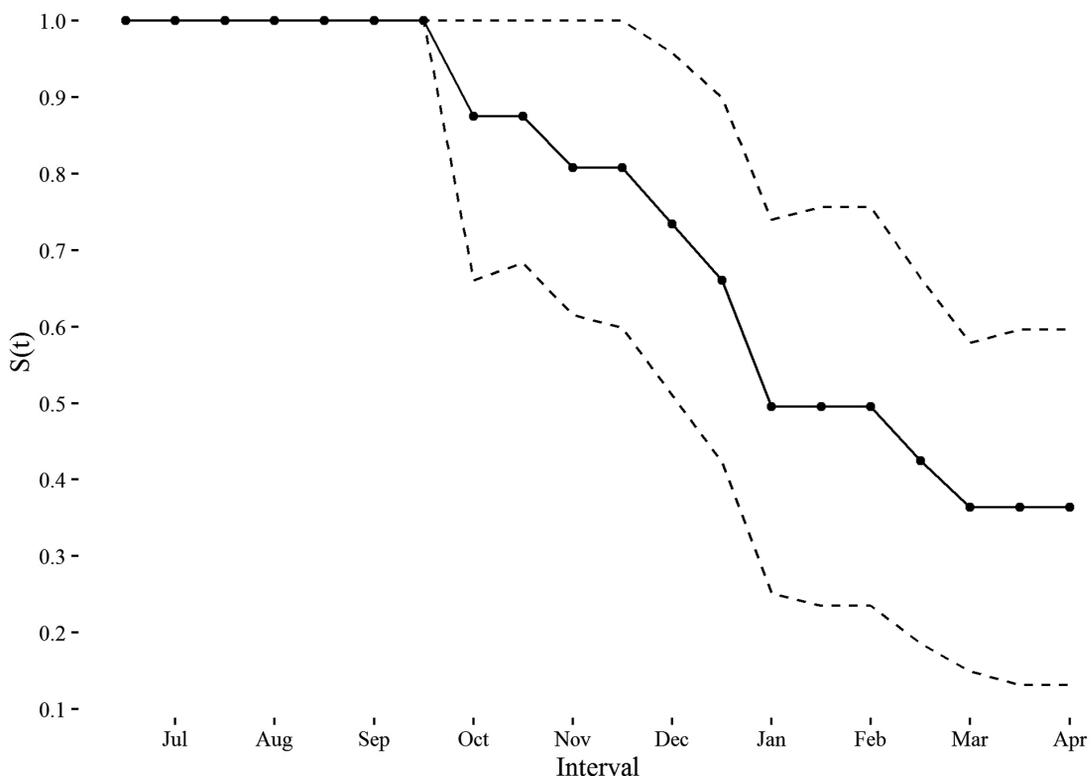


Figure 1. Estimates of biweekly null model Kaplan-Meier cumulative survival of short-tailed on the MacDonald-Dunn study area, Benton County, Oregon, 15 June 2012–1 April 2013. Solid dots indicate 2-week survival estimates and dashed lines indicate 95% confidence intervals.

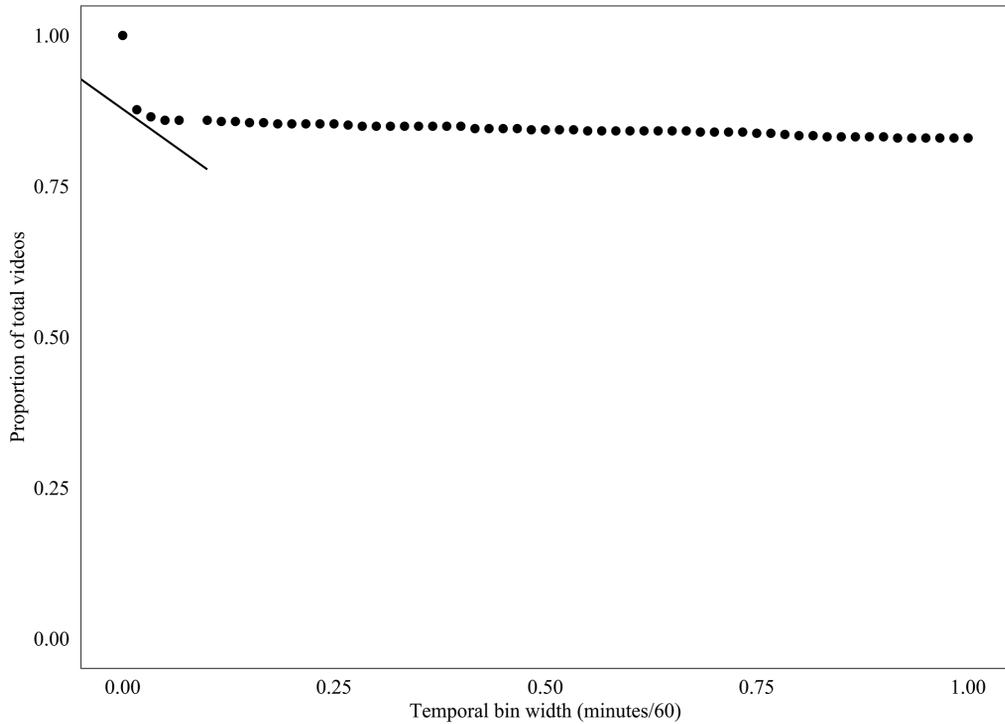


Figure 2. Number of remote camera videos of short-tailed weasels (*Mustela frenata*) per temporal bin width (total videos = 512, temporal bin width = 0) whereby only one video per bin was considered to be independent, i.e. for a 60-minute temporal bin width only videos > 60 minutes apart were counted. The line indicates where the slope of the the tangent approaches -1 .

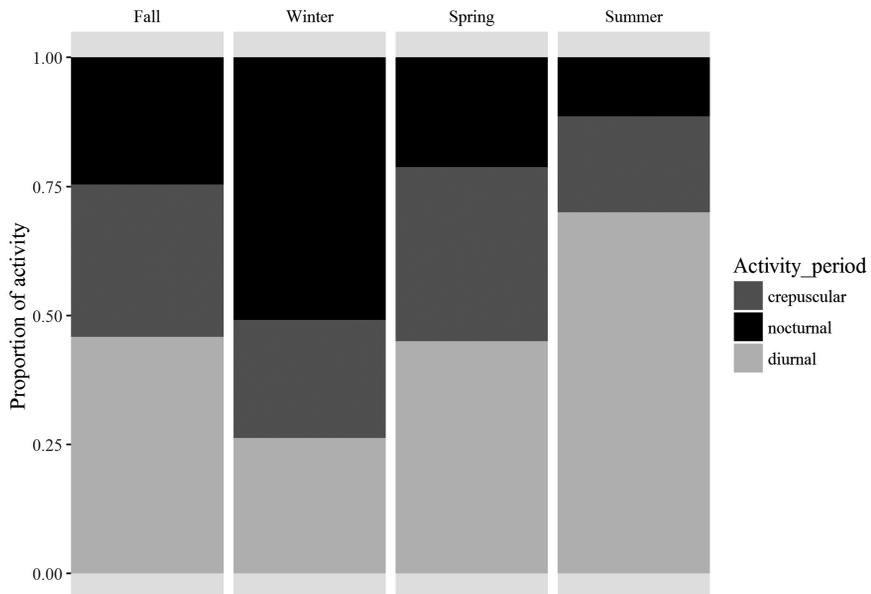


Figure 3. Proportion of activity during different times of day based on number of detections of short-tailed weasels observed by remote cameras placed at resting sites and trap sites on the MacDonald-Dunn Study Area, Corvallis, Oregon in 2012–2013. Activity is divided into 3 bins: diurnal, crepuscular (1 hour before and after sunrise and sunset), and nocturnal. Number of detections: Fall ($n = 61$), Winter ($n = 57$), Spring ($n = 70$), Summer ($n = 235$).

Literature Review of Weasel Studies

In total, 99 weasels and 15 predation events were observed across all studies, and six of seven studies reported predation on weasels. The daily predation rate was 0.0028 ± 0.0017 : i.e., each day of the year, on average, a weasel had a 0.28% chance of being killed by a predator. Using the mean daily survival rate, the annual survival index of weasels based on the combined data from our study and the six other studies that we reviewed was 0.37 ± 0.28 . Seven mortalities of short-tailed weasels caused by predation were documented in 2916 tracking-days; five were due to predatory birds, one was a bobcat (our study), and one was an unknown mammal. In 2542 tracking-days of long-tailed weasels, of eight confirmed mortalities in which cause was determined to be predation three were attributed to predatory birds, two were attributed to mustelids, and three were killed by other mammals. Combining both species, weasels were killed by predators $> 2x$ more frequently in winter (seven predation events in 1605 tracking-days, $n = 4$ studies) than in summer (eight predation events in 3846 tracking-days, $n = 7$ studies, Table 1). Predatory birds were responsible for the majority (six of seven; 86%) of predation events in winter. Mammalian carnivores, including two predation events attributed by the author to mustelids (Gehring and Swihart 2000, Richter 2005), accounted for six of eight (75%) predation events in summer (Table 2). Unidentified carnivores (< 5 kg) were suspected in three of the four predation events that were attributed to mammals in summer (Caroline St-Pierre, Université du Québec à Rimouski, personal communication); the fourth event was a coyote (Richter 2005).

Discussion

Annual survival of weasels in our study (0.26) and the average annual survival index estimated from our study and published studies combined (0.37 ± 0.28) approached the threshold survival rate below which Powell's (1973) model demonstrated that weasel populations could be limited by predation (i.e., survival ≤ 0.30). Moreover, we may have underestimated actual survival in our index because weasels were killed at a higher rate in winter and

most studies were conducted in summer. The cumulative results of our study and those conducted in Europe show that weasels were regularly killed by predators and frequently consumed (Korpimäki and Norrdahl 1989b, Jędrzejewski et al. 1995), and that predation rates may be high enough to limit many weasel populations.

We concluded that survival in our field study did not vary by sex or season, which was most probably due to small sample sizes which resulted in broadly overlapping confidence intervals. Across field studies, however, weasels were killed $> 2x$ more frequently during winter, providing evidence for a seasonal difference in predation mortality. Main predators differed by season with 75% of predation mortalities attributed to mammalian predators in summer and 86% to predatory birds in winter. In our field study, *M. erminea* exhibited greater nocturnal activity in winter representing a shift from strongly diurnal activity in summer. Predation mortality in winter was attributed to barred owls from weasel remains found in owl pellets. We concluded that: 1) predation rate and main predators varied by season, and was higher in winter when predatory birds were the main predator, and 2) in our field study, weasels may have been more vulnerable to nocturnal predators in winter because of greater nocturnal activity compared to other seasons.

Seasonal predation by predatory birds and mammalian predators, observed in our study, may have resulted from different predator motivations—consumption by predatory birds and incidental killing by mammalian predators—and has consequences for population limitation. In our field study, predatory birds during winter consumed the weasels they killed, and the one mammalian predator left the weasel carcass intact. Furthermore, across studies terrestrial mammals including other weasels were the primary predators of weasels during the summer breeding season. We propose that summer mortality due to mammalian competitors, including other weasels, may frequently represent incidental predation (St-Pierre et al. 2006) and may be an outcome of increased breeding season movements by male weasels (Erlinge and Sandell 1986) leading to increased

encounter rates with other breeding terrestrial mammals. In contrast, we propose predatory birds primarily cue into weasels as prey, particularly when other prey becomes scarce (Korpimäki and Norrdahl 1989a), as often occurs during winter in North America. Although weasels are not typically primary prey for predatory birds, and occur relatively infrequently (< 1%) in predatory bird diets (Craighead and Craighead 1956, Korpimäki and Norrdahl 1989a, Wiens et al. 2014), in times of scarcity weasels may constitute a much greater proportion of predatory bird diet (Korpimäki and Norrdahl 1989a). Therefore, we propose that predation resulting in consumption, indicating motivation by the predator, may thus represent the mechanism most likely to exhibit the strongest limitation on weasel populations in North America, and that this pressure may increase seasonally or during years of scarcity.

In our field study, most weasels were found killed and consumed by barred owls. In the western Oregon Coast Range, barred owls have expanded into more vegetation cover types (including managed forests), and occur at higher densities than native spotted owls (*Strix occidentalis*), consuming more weasels (~ 1.8% vs. 0.3% of prey in diet) and *Microtus* voles (2% vs. 0.9%) than spotted owls (Wiens et al. 2014). We suggest, therefore, that barred owls have the potential to limit weasel populations locally, and that continued direct

investigation of barred owl-weasel interactions in western Oregon may be warranted.

Long term data sets examining interactions between weasels, their predators, and shared prey are rare (Erlinge 1983, Erlinge et al. 1984). Addressing hypotheses of the effects of predators, specifically predation and exploitative competition (reductions in shared prey), will almost certainly involve integration of field data with mathematical models. A next step might be to update Powell's (1973) model, using survival estimates from this study and scenarios that examine the effects of seasonal survival and prey availability on reproductive output and population growth rate.

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