PREDATION ON MEADOW VOLES: PREDATOR RESPONSE TO VOLE ABUNDANCE AND VOLE RESPONSE TO PREDATOR EXCLUSION IN RED ROCK LAKES NATIONAL WILDLIFE REFUGE, MONTANA

by

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Joel Ryan Burgener
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ABSTRACT

Small mammals such as meadow voles exhibit complex and puzzling multi-annual population cycles. Predators can have an effect on these cycles though the precise relationship is not completely understood. I undertook this study to 1) quantify the response of predators to small mammal abundance and 2) determine the relative roles of mammalian meso-predators and raptors on abundance and survivorship of small mammals in wet meadow habitat at Red Rock Lakes National Wildlife Refuge, southwest Montana. as well as the response by predators to different levels of small mammal abundance. Two randomly placed trapping grids were placed inside three adjacent grazing units. Two additional treatment trapping grids were placed inside one of the grazing units with an electrified polywire fence to exclude mesopredators. The trapping occurred in July and August of 2010 on the Refuge. The trapping occurred in three primary sessions with four individual trapping days (secondary sessions) per primary session in each grazing unit. Predators were monitored by conducting visual raptor surveys and camera trapping. My results indicated that partial predator exclusion did not improve vole survivorship in fact some raptors used the fence posts as supplemental perches, as some bore signs of use. My results also did not support the hypothesis that raptor abundance tracked vole abundance. However, vole abundance was significantly higher during 2010 than in previous years. The increase in vole abundance resulted in other factors driving habitat selection by raptors. The camera traps did not provide any information about the use of the wet meadow by mammalian predators, however other signs of mammalian predators were observed in the trapping area during the study. Further study may shed more light on the use of supplemental perches by raptors and how mammalian predators are using the wet meadow habitat on the Refuge.

INTRODUCTION

Small mammal communities, namely microtines, are notorious for exhibiting multi-annual population cycles (Getz et al. 2001; Hanski et al. 2001; Krebs et al. 1969). Several competing hypotheses have been proffered to explain these cycles. The plant-herbivore hypothesis suggests population cycles are tied to plant-food resources (Krebs et al. 1995), while the predator-prey hypothesis postulates that predation can either produce or moderate these cycles in the predator-prey hypothesis(Baker & Brooks 1981; Ekerholm et al. 2004; Krebs et al. 1995; Reid et al. 1995). The conflict between the "bottom-up" plant-herbivore hypothesis and "top-down" predator-prey hypothesis likely oversimplifies the complex factors that lead to the observed population cycles (Krebs et al. 1995). It seems unlikely predators have little to no influence on small mammal population cycles (Korpimaki & Krebs 1996; Krebs et al. 1995). A resident, specialist predator can destabilize prey numbers by increasing the magnitude of the periodic population cycle, whereas a generalist or migratory predator can dampen the amplitude of prey population cycles (Korpimaki & Krebs 1996). For example, migratory avian predators such as short-eared owl (*Asio flammeus*) often respond numerically to seasonal changes in small mammal abundance, which can lead to localized reductions in small mammal abundance (Norrdahl & Korpimaki 2002). Conversely, coyote (*Canis latrans*), a territorial generalist, can stabile snowshoe hare (scientific name) populations by increasing the number of kills per day only when the population cycle was at or near a peak (O'Donoghue et al. 1998). Least weasels (*Mustela nivalis*) are a specialist predator that has demonstrated destabilizing effects on populations of field voles (*Microtus* *agrestis*) in Fennoscandia by maintaining its hunting pressure even during low points in the population cycle (Hanski et al. 1991). One way to better understand the role of a predator in prey abundance and survival is to exclude some or all predators in a given area. In a study conducted by Korpimaki et al (2002), reduction of predators had an impact on each phase of the population cycle of voles, including increasing the density in a low phase, accelerating the increase leading to an increase in the peak phase of the cycle and delaying the decline from the peak.

Predators can demonstrate a functional or numerical response to vole abundance or density. A functional response by a predator is characterized by a change in behavior in response to prey abundance. For example, a territorial species may use an area of its territory with more frequency if prey is more abundant in that area. Generalist predators such as coyote can quickly locate small patches of their territory with higher densities of voles (Lin & Batzli 1995). Coyotes in particular have been shown to consume in proportion to abundance of particular prey species (Bartel & Knowlton 2005). A numerical response is a change in predator abundance paralleling a change in prey abundance or availability. Predators may concurrently demonstrate a numerical and functional response to prey abundance. Short-eared owls have been shown to demonstrate a numerical response to vole abundance by over-wintering in areas in significantly greater numbers in years when vole abundance was high (Baker & Brooks 1981).

OBJECTIVES

The objectives of this study were to 1) investigate the response of small mammal abundance and survival to the exclusion of some mammalian predators in wet meadow habitats on Red Rock Lakes National Wildlife Refuge (hereafter Refuge) and 2) investigate the effect of predator numerical response to vole abundance. Additionally, this study provided insight into the use of the wet meadow habitats on the Refuge by mammalian and avian predators, as well as suggested hypotheses to be investigated in future studies.

STUDY AREA

The study was conducted on Red Rock Lakes National Wildlife Refuge in southwestern Montana. The Refuge encompasses 18,210 ha of the Centennial Valley, with elevations ranging from 2013 m above mean sea level (msl) to > 2926 m msl. Average annual precipitation, as measured at Refuge Headquarters (2039 m msl), is 49.5 cm with 27% occurring during May and June. Annual average temperature is 1.7° C. The wet meadows of the Refuge are grazed on a three-year grazing cycle. The current grazing management plan calls for a minimum of 2 full growing seasons of rest between grazing treatments. Cattle are put on units no earlier than 10 July of the third year since last grazed.

Wet meadows are rare, ecologically important habitats in the arid and semi-arid Intermountain West. For the purposes of this study, we defined wet meadow habitat as the *Juncus balticus – Carex praegracilis* vegetative alliance (National Vegetation Classification Standard [NVCS]). Wet meadows are an ecologically diverse habitat that commonly results from a perched water table that sub-irrigates the plant community, supporting high primary productivity and a diverse faunal community (Laubhan 2004). Riparian habitats such as wet meadows make up less than 2% of the surface area of the Intermountain West (Lohman 2004). Small mammals occur in greater abundance with greater species richness in these riparian areas (Lohman, 2004). Mammal populations found in Intermountain West wet meadow habitats include montane voles (*Microtus montanus*)and meadow voles (*M. pennsylvanicus*), deer mice (*Peromyscus maniculatus*), vagrant shrews (*Sorex vagrans.)*, and common shrews (*S.x cinereus*). Voles occur in greater abundance in the wet meadow habitat than the surrounding drier uplands due to increase in moisture which supports greater numbers and variety of plants and insects as well as soil more suitable for burrowing (Lohman 2004; Sullivan 1996). The diversity and abundance of small mammals supports an equally diverse predator community in wet meadows including small to medium sized mammals in addition to avian predators. Predatory mammals that have been spotted in the study area include least weasel, badger (*Taxidea taxis*), coyote, red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*), and more recently wolves (*Canis lupus*). Avian predators include, but are not limited to, northern harriers,red-tailed hawk (*Buteo jamaicensis*) and short-eared owl.

METHODS

Small Mammal Abundance and Survival in Response to Predator Exclusion

Small mammal abundance and apparent survival were estimated between control and treatment groups following capture-mark-recapture methods. Two trapping grids per group were established within wet meadow habitat. Grids consisted of 100 Sherman® live traps spaced 15 m apart within a 10 x 10 grid. Control group grids were randomly placed within a Refuge grazing unit in 2007 and have been studied since that time (Whelham 2008). The treatment grids were placed ~400m from each of the control grids on approximately the same northing as the associated control grid, though the Treatment North grid was adjusted to prevent setting up traps in standing water (Table 1). Effective trap area for my study site was estimated to be 2.24 ha (Whelham 2008).

An electrified fence was used to exclude mammalian meso-predators from the treatment group, primarily coyote, red fox, and striped skunk. Fences were comprised of equidistantly placed posts that held four strands of poly-wire (Gallagher USA, Kansas City, MO) spaced ≈ 15 cm apart with the bottom strand eight cm above the ground. The fence was electrified using a 12 volt battery charged by a solar panel.

I used a robust design sampling scheme to concurrently estimate small mammal abundance and apparent survival (Pollock 1982). Trapping was conducted during three primary trapping occasions, each comprised of four secondary occasions. Secondary occasions occurred consecutively within each primary session such that each primary session was four days long. Primary occasions were separated by 12 days. Traps were opened each evening no earlier than 1700 hours and traps were checked the following morning starting no later than 0900 hours. Each animal captured was marked with a uniquely numbered ear tag (size 1005-1, National Band and Tag Company, Newport, KY). Species, sex, evidence of reproduction (pregnant female, lactating female, male with enlarged testes, and no evidence), and release status (dead, injured, or unharmed) were recorded. Morphometrics taken on individuals included total length (± 1 mm), tail length (± 1 mm), and mass (± 1 g). Tag number and reproductive status were recorded for recaptured animals.

Table 1. Trapping grid locations for Control vs. Treatment small mammal trapping at Red Rock Lakes, NWR, 2010. The northeast corner of the trapping grid is represented by the intersection of the listed Northing and Easting. All locations are NAD83 datum.

Trapping Grid	Northing	Easting
Control North	4945781	442021
Control South	4945042	441998
Treatment North	4945081	443047
Treatment South	4944751	442688

Predator Community Composition and Response

Raptor abundance was estimated via raptor surveys conducted at each grid each trapping day immediately prior to checking traps in the morning and opening traps in the evening. Observers recorded species, sex (when identifiable), and behavior (foraging, territory defense, display flight) for all raptors observed during a five minute point count conducted at the trapping grid. In addition to the four trapping grids used to explore the influence of functional versus numerical predator response on small mammal abundance, four additional grids were monitored concurrently as part of an ancillary study (Table 2). These grids were located in three different cattle grazing units, 15A, 15B, and 15C

(Figure 1). These grids were monitored following the same protocol as the four original grids.

I employed camera traps in an effort to document the predator community on the study site. Camera traps offer a non-intrusive method of obtaining information about the mammalian predators present during the trapping period. Cameras were placed in each of the three grazing units, with two cameras per trapping grid placed 200 m from the center of the trapping grid on a random bearing. I believed this distance to be close enough to the trapping grid to capture the predator community within the area without attracting predators to the trapping grid. The cameras were baited using urine-scented trapping lure and feces of domesticated dogs (*Canis familiaris)*. In addition to camera traps, the adjacent sand/dirt road was occasionally dragged and monitored for tracks.

Table 2. Trapping grid locations for small mammal trapping of additional grazing units at Red Rock Lakes, NWR, 2010. Corner UTM lists which corner of the grid is indicated by the intersection of the easting and northing UTMs. All locations are NAD83 datum.

Grazing Unit	Easting	Northing	Corner UTM
15A	447154	4943988	NE
15A	445523	4943776	SE
15B	444548	4943835	SE
15B	442912	4944468	NE

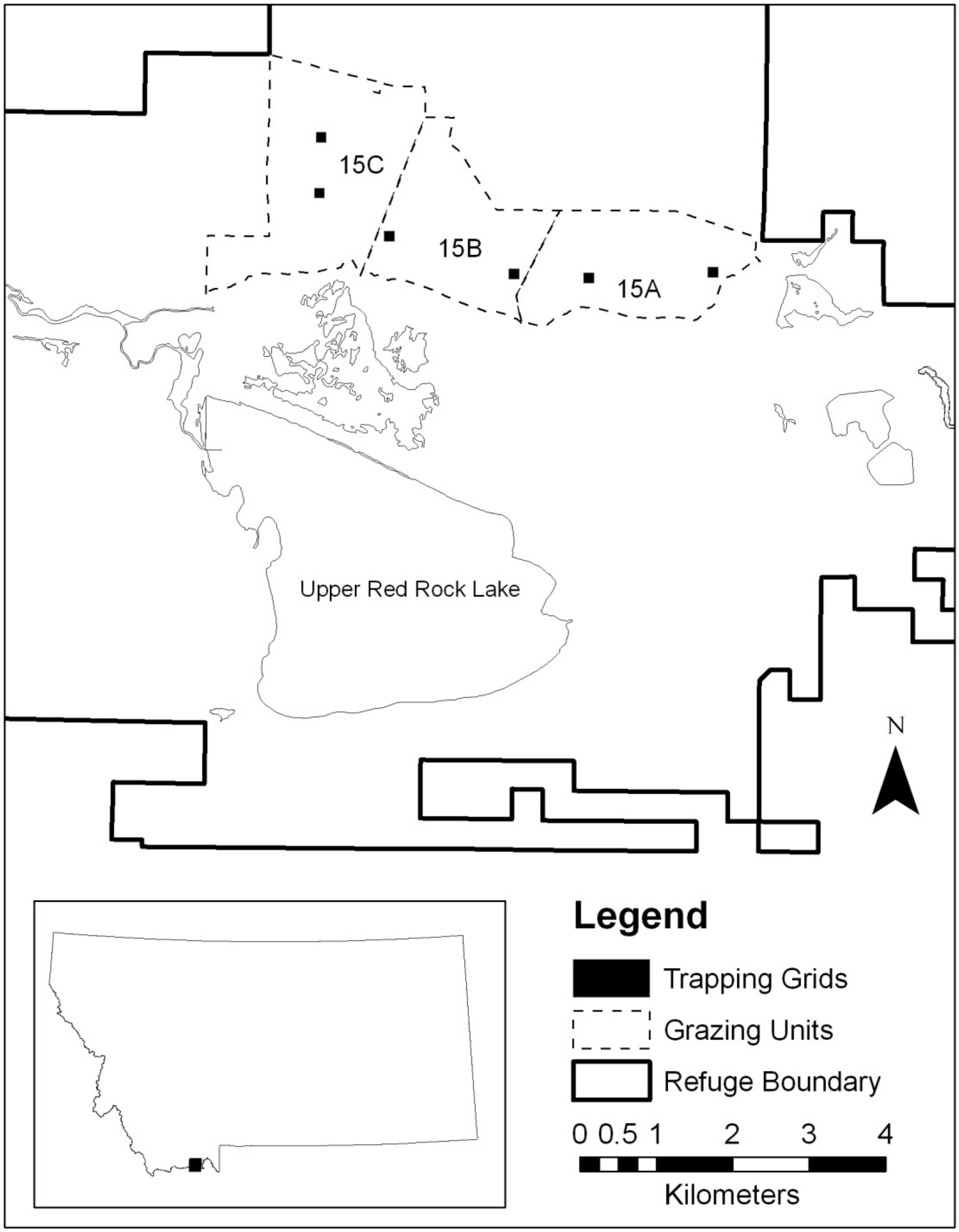

Figure 1 .Location of study area, grazing units, and small mammal trapping grids at Red Rock Lakes National Wildlife Refuge, Montana. Inset map shows the location of Red Rock Lakes within Montana.

DATA ANALYSIS

Abundance and Apparent Survival of Small Mammals

Capture-mark-recapture data were analyzed using Robust Design models (Pollock 1982) in Program MARK (White and Burnham 1999). I compared models with group apparent survival (ϕ) constant and time-varying (t), as well as models without a group effect. To determine the most parsimonious apparent survival model, I ranked candidate models using Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson 1998). I estimated a model-averaged vole abundance using Huggin's conditional likelihood (Huggins 1991; Huggins 1989). Model averaging was done by weighting each based on its ΔAIC_C with the smallest ΔAIC_C getting the most weight (Buckland et al. 1997). Model averaging was not used in calculations for apparent survival. I similarly estimated small mammal abundance for each grazing unit to explore the numerical response of raptors to small mammal abundance. However, model averaging was not appropriate with that data set as there was not significant model uncertainty.

Data from the grids in 15A, 15B, and unfenced 15C were analyzed in the same manner though completely independently. Vole abundance and survivorship was estimated using grazing unit as a categorical covariate.

Camera Trap Analysis

Photos taken by camera traps were checked for the presence of predator species. It was my intention to compare mean number of predator species spotted by camera traps by grazing unit. However, the cameras only captured non-predatory mammals and owls in the photos, precluding such analysis. Other evidence such as recently used dens, scat, tracks, and vocalizations indicated the presence of predatory species in the immediate vicinity. However, the lack of photos prevented any quantitative assessment regarding these predators used the wet meadow habitat.

Raptor Survey Analysis

Daily raptor sightings were summed (morning and evening surveys) and then analyzed for differences among grazing units in each session using generalized linear models, a log link, and a Poisson distribution of errors in R 2.8.1 (R Development Core Team 2008).

RESULTS

Small Mammal Trapping in Treatment and Control Grids

Trapping efforts resulted in the capture of 783 animals, 781 voles (*Microtus* spp.) (99.7%) and 2 shrews (*Sorex* spp.) (0.3%). There were 122 recaptures. Most of the individuals were captured (63.5%) and recaptured (62.3%) in the control grids.

There was considerable model uncertainty in my model set with four models within 2 AIC_c units of each other (Burnham and Anderson 1998) (Table 3). My most parsimonious model indicated no difference in survival between grids where mammalian meso-predators were excluded and control grids. In both of these models, capture and recapture probability varied by primary and secondary session.

The next two models are also competitive models. These two also show very little difference between the time-varying and group varying apparent survival. These two models are similar to the top two models but differ in that these set the recapture probability for each session to be constant throughout and equal to the capture probability of the last day of that primary session.

Table 3. Ranking of Robust Design mark-recapture models investigating effects of partial predator exclusion on vole apparent survival (ϕ),, capture (p), and recapture I probabilities. I tested models where ϕ,, p, and c were constant or varied with time (for p and c this was by session and days within session (t), by session only, and by days within session only). I also tested models where p and c were equal as well as setting c to a value equal to the last capture probability of each primary session shown as "c=p $_{day4*session}$". For all models present, immigration(γ')and emigration (γ'') is fixed to 0..

Model Structure	Δ^a AIC$_c$	w^b	k^c
ϕ_t p_t=c_t	0	0.29147	14
ϕ_g p_t=c_t	0.44	0.23391	14
ϕ_t p_t c=p $_{day4*session}$	1.4325	0.14241	14
ϕ_g p_t c=p $_{day4*session}$	1.7444	0.12184	14
ϕ_t p_t $c_{session}$	3.2284	0.05802	15
ϕ_{g*t} p_t= c_t	3.8137	0.0433	16

[a]Difference between present model and best model.
[b]Normalized relative model likelihoods
[c]Number of estimated parameters

Vole abundance in the treatment peaked in the second primary session (603.0± 147 SE), which was a considerable increase from the first primary session (31.0±14 SE), before a small decline in the third primary session (481.3± 69 SE). The control group increased in abundance over the entire trapping season with a large increase from the first primary session (172.2±66 SE) followed by a slight increase between the second primary session (776.7± 187 SE) and the third primary session (862.5±120 SE) (Figure 2).

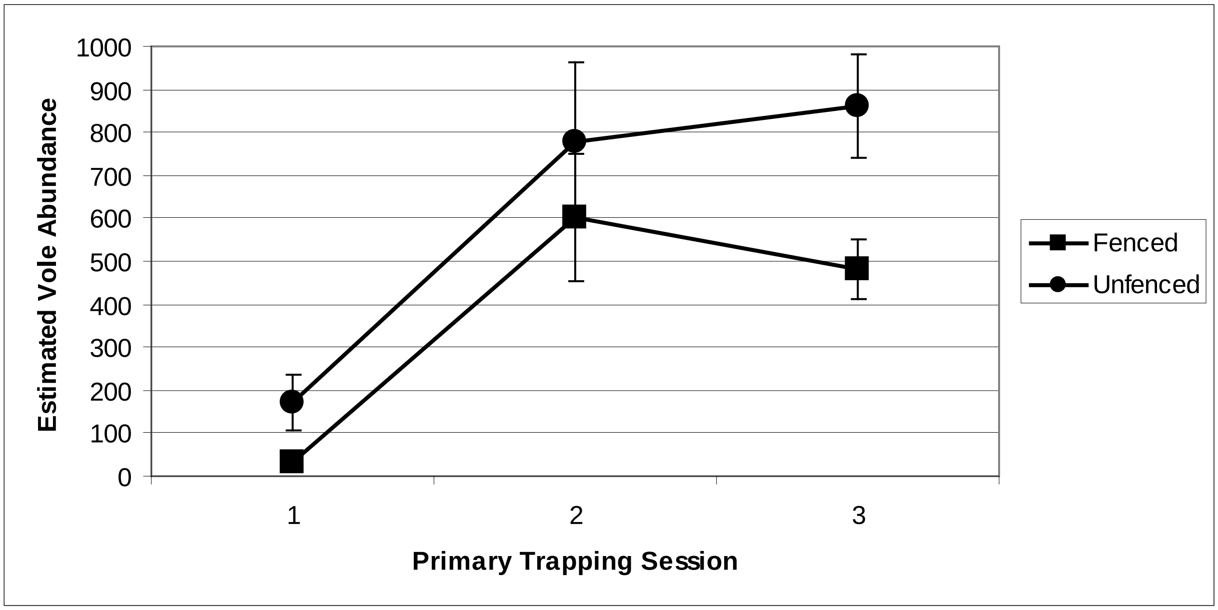

Figure 2. Model averaged estimates of vole abundance (±1 SE) by treatment group and primary trapping session in wet meadow habitat, Red Rock Lakes NWR, 2011.

The most parsimonious model indicated that apparent survival did not vary between the treatment and control groups, hereafter group invariant model. Apparent survival in the group invariant model indicated increased apparent survival over the season with apparent survival between the first primary session (.34±.14 SE) and the second primary session (.54± .09 SE) (Figure 3). A second competitive model (ΔAIC_c =0.44) showed a small but insignificant difference in apparent survival between the treatment and control group, hereafter group variant model. Apparent survival in the group variant model indicated greater apparent survival in the control group (.54 ± .11 SE) over the fenced treatment group (.45±.08) (Figure 4).

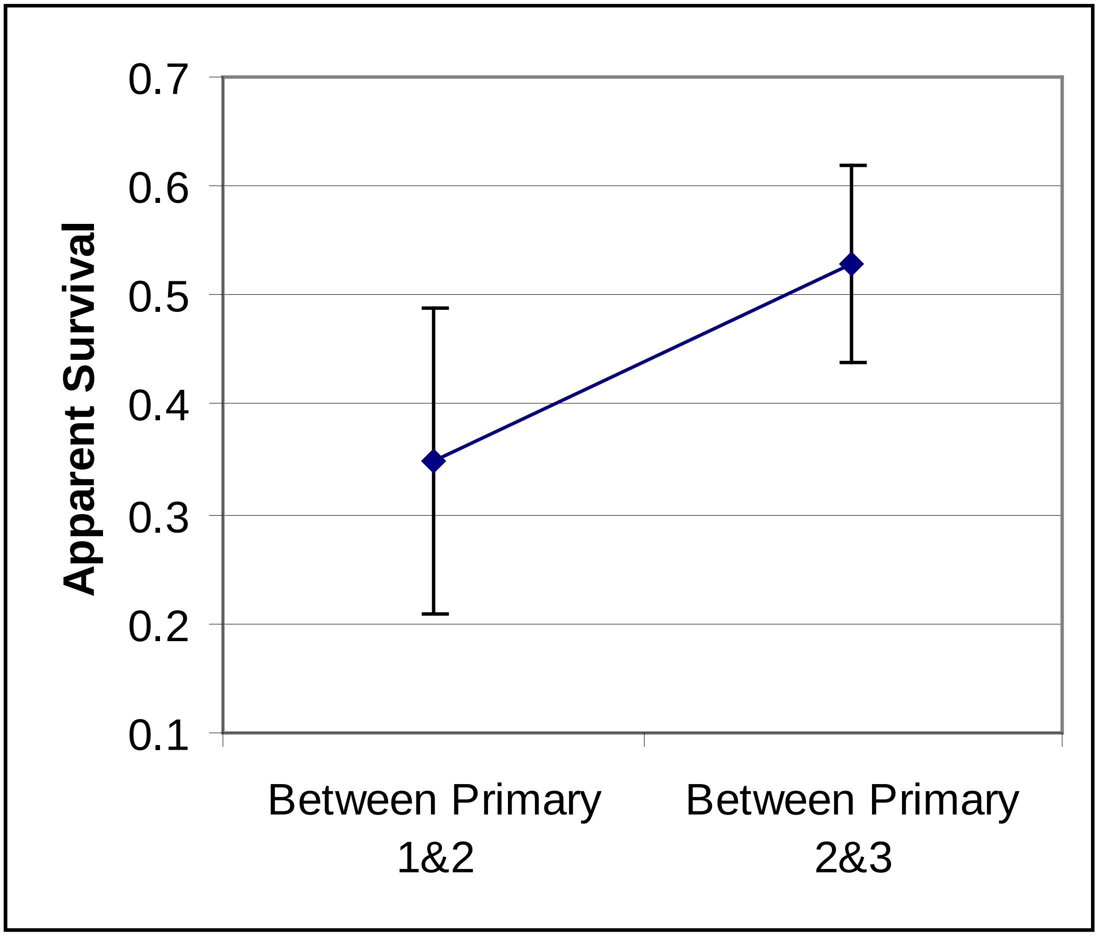

Figure 3. Group invariant model estimates for apparent survival (±1 SE) between primary trapping session 7/10/2010-7/23/2010 and 7/27/2010-8/9/2010 respectively in grazing unit 15C, wet meadow habitat, Red Rock Lakes NWR, 2011.

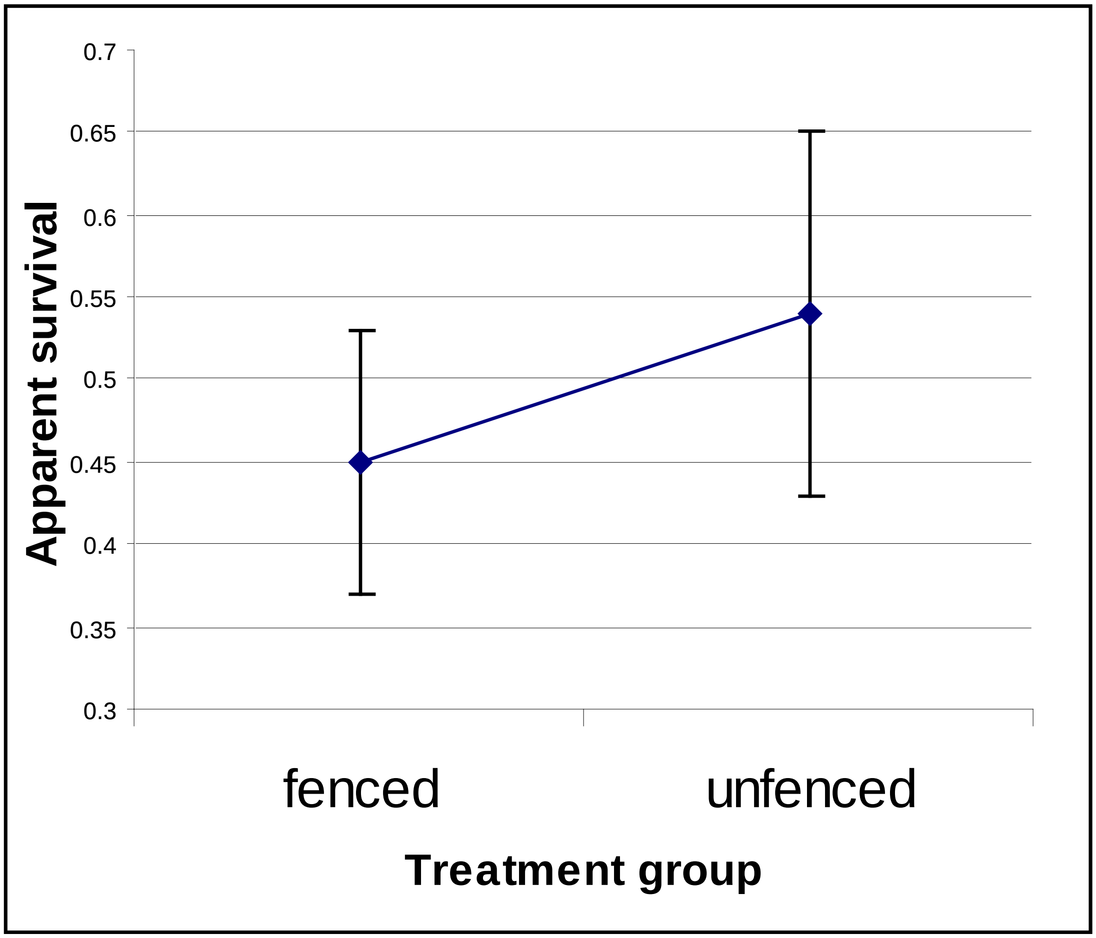

Figure 4. Group variant model estimates for apparent survival (±1 SE) by treatment group in grazing unit 15C, wet meadow habitat, Red Rock Lakes NWR, 2011.

Raptor Surveys

Raptor survey data showed relative stability in the number of raptors using each of the different grazing units with the exception of the third primary session. In the final primary trapping session only 15B continued to be stable while 15A and 15C showed declines in the number of birds spotted (Table 4). Unfortunately, the survey data for the third primary session in 15C was suspect. In addition to an exceptionally low count, data sheets were not completely filled in, suggesting final counts were not tallied on the appropriate sheets. Though the surveys were never conducted on the fenced trapping grids, as many as six short-eared owls could be seen hunting the fenced grid on one particular evening during the third trapping session, as well as one northern harrier each morning of the third trapping session. While it is obvious the count for the third primary trapping session of 15C should be higher, it is impossible to specifically know by how many.

Table 4. Total number of raptor sightings by primary trapping session in each grazing unit, wet meadow habitat, Red Rock Lakes NWR, 2010.

Grazing Unit	Session 1	Session 2	Session 3
15A	17	18	9
15B	16	25	25
15C	18	20	2

Table 5. Total number of small mammals captured annually in a wet meadow habitat at Red Rock Lakes NWR 2007-2010. The same trapping grids were used each trapping year. The additional predator exclusion grids from 2010 were not included in this animal count.

Trapping Year	Number of Animals Captured
2007	346
2008	195
2009	356
2010	1330

<u>Small Mammal Trapping of Adjacent Grazing Units Relative to Second Objective</u>

Vole abundance and apparent survival between grazing units was estimated based on the most parsimonious model. This model indicated the following: apparent survival varied by both time interval and grazing unit, capture probability varied by grazing unit and by day of the primary session but that pattern remained constant between primary sessions, and recapture probability varied by group but was constant for each group and was equal to the capture probability of the last day the trapping session(Table 6).

Table 6. Ranking of Robust Design mark-recapture models investigating differences between grazing unit on vole apparent survival (ϕ)capture (p), and recapture I probabilities. I tested models whereϕ, p, and c were constant or varied with time (for p and c this was by session and days within session (t), by session only, and by days within session only). I also tested models where p and c were equal as well as setting c to a value equal to the last capture probability of each primary session shown as "c=p $_{day4*session}$". For all models present, immigration(γ')and emigration (γ'') is fixed to 0

Model Structure	Δ[a] AIC_c	*w*[b]	*k*[c]
$\phi_{g*t)}$, $p_{(g*days)}$, c=p $_{day4*session}$	0	0.88764	18
$\phi_{g*t)}$, p_{g*days}=$c_{(g*days)}$	5.6019	0.05393	18
$\phi_{g*t)}$, p_{g*days}, $c_{(g*days)}$	6.4518	0.03526	27
ϕ_{g*t} p_t= c_t	10.9908	0.00364	18

[a]Difference between present model and best model.
[b]Normalized relative model likelihoods
[c]Number of estimated parameters

The most parsimonious model of differences among grazing units indicateds units 15A and 15C increased in vole abundance over the course of the trapping sessions, while 15B peaked in the second session and had a steep decline in the third session (Figure 6). Apparent survival decreased over time in groups 15A and 15B, but increased in 15C. At the end of the season, 15C had the greatest abundance of voles and the greatest level of apparent survival (Figures 5 & 6).

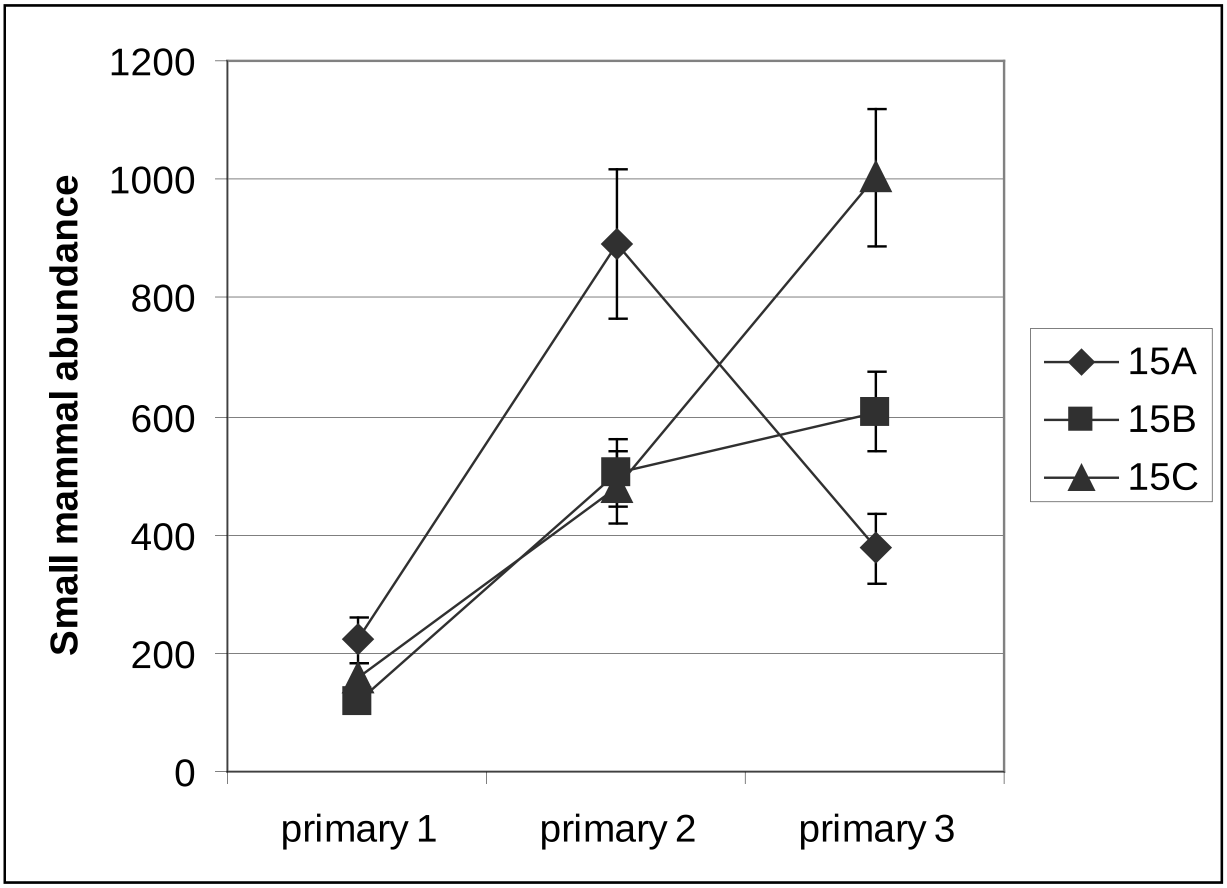

Figure 5. Vole abundance (±1 SE) by grazing treatment and primary trapping in grazed wet meadow, Red Rock Lakes NWR, 2010.

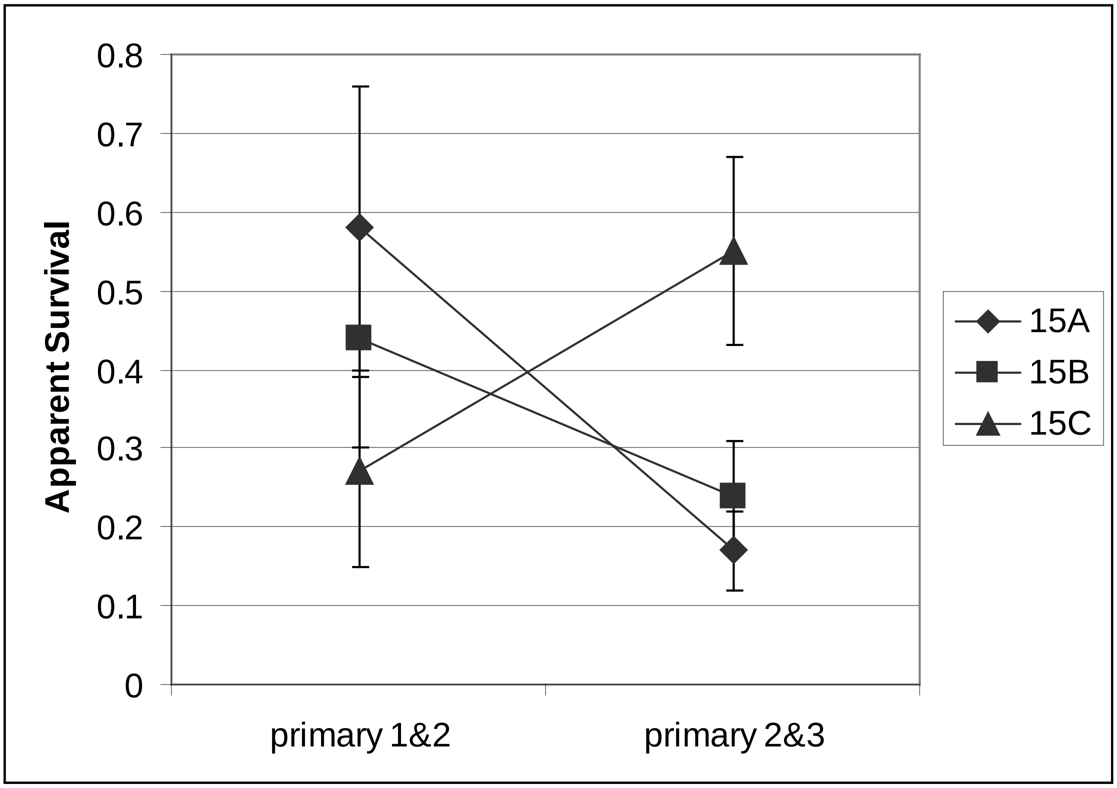

Figure 6. Apparent survival (±1 SE) by grazing treatment in grazed wet meadow at Red Rock Lakes NWR, 2010. Primary 1&2 represents the time gap between the first two primary trapping occasions for 15A (7/6/2010-7/19/2010), 15B (7/2/2010-7/15/2010), and 15C (7/10/2010-7/23/2010). Primary 3&4 represents the time gap between the second and third primary trapping occasions for 15A (7/22/2010-8/5/2010), 15B (7/18/2010-7/31/2010), and 15C (7/27/2010-8/9/2010)

Camera Traps

The remote monitoring by camera traps yielded no photo evidence of predatory mammals in the area around the trapping grids or inside the treatment grids, despite baiting of cameras. It is evident that predatory species were present in the area where trapping occurred, however. Canid tracks were found on a groomed dirt road adjacent to grazing unit 15C headed in the direction of the grazing unit (Figure 7). Additionally, at least one den marked by coyote scat was located near the trapping grids in 15 C (Figure 8). Photos of pronghorn (*Antilocapra americana*) and short-eared owls were taken (Figure 9).

Figure 7. Canid tracks on groomed dirt road adjacent to grazing unit 15C. Photo taken on July 19, 2010 at Red Rock Lakes NWR.

Figure 8. Coyote den, marked by scat, in grazing unit 15C. Photo taken on July 22, 2010 at Red Rock Lakes NWR.

Figure 9. Pronghorn, top, and short-eared owl, bottom, photos taken by different camera traps July 27 and 23, 2010, respectively, in grazing unit 15B at Red Rock Lakes NWR.

DISCUSSION

Predators may be the most significant factor in vole population cycles (Ekerholm et al. 2004). Altering predator access to prey would impact prey survivorship and abundance(Krebs et al. 1995). By reducing access of two 2.25 ha areas to meso-predators, I predicted that vole survivorship would be greater than in corresponding areas with no such access limitation. The data was contrary to this. The mitigation of an effect by the fencing likely was due to the general abundance of voles. This season's estimates for abundance were so significantly higher than the previous seasons, it is unlikely that predation significantly affected vole abundance or apparent survival. Territorial species, like coyotes, would be swamped by the number of voles and addition of coyotes from outside the territory would be unlikely. Additionally, camera traps did not capture photos of other coyotes entering the territory. This year, it does not appear that the raptors favored any grazing unit in particular. Despite evidence in previous studies of the Refuge (Reed 2009), raptor distribution across the grazing units did not seem to track with varying abundance of small mammals. This is also likely due to the abnormally high number of total animals captured this year. 2010 showed a 274% increase in voles from the previous year (Table 5). In fact, 2010 captures represented a nearly 50% increase in the number of animals captured in 2007-2009 combined. This population boom may have minimized any effect relative abundance would have on raptor distribution. However, the presence of the supplemental perches on the treatment grids may have increased hunting success and had an impact of survivorship between the treatment/control units.

In order to further understand the predator-prey relationships on the Refuge, future studies should focus on more detailed reports of the ways that predators are using the Refuge. Continued raptor surveys with greater and/or more varied sampling times may provide more detail about where the birds are spending time. Camera trapping procedures should be improved to place the camera traps along game trails near the small mammal trapping grids rather than random GPS coordinates. Additionally, trapping and GPS-collaring of coyotes may yield an accurate picture of how the coyotes are using their territory. It will also be of great value for the small mammal trapping to continue to be done as it has since 2007 to continue to build a better picture of the multi-annual population cycles of voles. The 2010 trapping season marked a significant peak in the population. As the population declines, or drops precipitously, the information gathered will be valuable to understanding more about the predator-prey relationships at Red Rock Lakes National Wildlife Refuge.

MANAGEMENT IMPLICATIONS

Small mammals are key prey for many raptors. In order for the Refuge to manage for a diverse population of raptors, it is important to understand the relationship between the raptors and vole populations. At this time there is no evidence to support the use of meso-predator exclusion to improve vole survivorship, although the drastic peak in vole abundance may belie the actual impact of meso-predators have in years with lower numbers of small mammals. The presence of owl pellets at the base ofon treatment fence posts and camera trap posts indicates that raptors will make use of supplemental perches on the refuge. Such perches might be successful in alleviating hunting pressure near current perch sites such as fence posts near the road and between grazing units.

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