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Final Report
For
Vertebrate Pest Control Research Advisory Committee

Study Title:
Encouraging owl predation of rodents by erecting owl
boxes: myth or potential management strategy?

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EXECUTIVE SUMMARY

Barn owls (*Tyto alba*) have become a popular component of Integrated Pest Management Programs in California to control rodent pests. Barn owls can be encouraged to hunt on farms by constructing artificial nest boxes, which are relatively cheap to establish and require little continued effort by farmers once owls have established. However, no data exists to support the contention that barn owls are capable of controlling populations of rodent pests that are often capable of rapid reproduction.

We used population matrices and predator-prey models to predict the utility of barn owls for controlling two common rodent pests of California farms, the pocket gopher (*Thomomys* spp.) and the vole (*Microtus* spp.). Specific details of our modeling methodology and findings include:

1. We used published data on pocket gopher and vole density, survival, and reproduction to construct multiple prey population matrix models to predict the intrinsic growth rates of populations with high, medium, and low growth. This provided a number of realistic contexts which were used to construct Rosenzweig-MacArthur predator prey models.
2. We used published data to determine likely barn owl population densities and to calculate the predation pressure of barn owls on prey populations.
3. Carrying capacity of the prey, density of barn owls, and underlying prey population growth parameters were all important in predicting the effects of barn owls on rodent pest populations.
4. Under all barn owl densities and pocket gopher or vole population growth rates, the addition of barn owl predation to the models resulted in rodent populations remaining below the environmental carrying capacity at the end of a 5-year time period.
5. Pocket gopher populations were always driven to extinction under the highest predation pressure from dense barn owl populations (1 or 2 pairs/ha). Under moderate barn owl population densities (0.6 pairs/ha), pocket gophers were driven to zero at the low and moderate pocket gopher population growth rates (r values of 0.01 and 0.28,

respectively), but were not driven to zero within the 5-year time frame at the highest pocket gopher population growth rates ($r=0.42$). At the lowest barn owl densities (0.2 pairs/ha), pocket gopher populations were never driven to zero in the 5-year timeframe.

6. At high barn owl densities (1 and 2 pairs/ha), barn owls were able to drive vole populations to extinction at low and moderate vole population growth rates. Only at the highest barn owl densities (2 pairs/ha) were barn owls able to drive vole populations to extinction when vole population growth rates were high. At moderate barn owl population densities (0.6 pairs/ha), owls were able to drive vole populations to extinction at very low vole population growth rates ($r=0.01$), were able to drive vole populations to 45-65% of K at moderate vole population growth rates ($r=0.7$), and were able to drive vole populations to 63-82% of K at high vole population growth rates ($r=1.45$). At the lowest barn owl densities (0.2 pairs/ha), owls were able to drive vole populations to 75-88% of K at moderate vole population growth rates ($r=0.7$), and were able to drive vole populations to 88-95% of K at high vole population growth rates ($r=1.45$).
7. It is important to note that our models were necessarily simplistic because of data limitations. We built single-species models but acknowledge that barn owls, pocket gophers, voles, and other rodents are often found together, and that barn owls are likely to switch from one prey species to the other depending on the abundance and accessibility of each species. Our models were based on data from multiple habitat types, and these models did not account for changes in prey behavior as a result of increased predation pressure.
8. Our models provide useful information on the likelihood that barn owls may control rodent pests, but we strongly encourage future studies to collect both barn owl and prey data simultaneously to derive the actual impacts of barn owls on their prey.
9. Through this study, we have greater insight for identifying scenarios where owls may have the ability to succeed at managing gophers and voles, and we've provided insight into the importance of certain variables for regulating population growth of rodents. By developing the framework for future modeling efforts, our study will be of significant

value to future field efforts to better understand the role of barn owls in the control of rodent pests.

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INTRODUCTION

Small mammal pests are an enduring challenge for farmers worldwide. Traditionally controlled by natural predators, habitat management, and trapping, small mammals are today often controlled by chemical rodenticides, which have become widespread and pervasive in some areas. However, rodenticides pose a challenge for farmers because they require continual applications over time (Engeman and Campbell 1999), may have decreasing efficacy if rodents become resistant to compounds (Salmon and Lawrence 2006), and some active ingredients may cause secondary poisoning in non-target animals (Christensen et al. 2012, Gabriel et al. 2012). Trapping, another common management technique, requires initial inputs (purchasing traps) as well as continued effort and associated staffing costs, but has been shown to be effective in the long term for pocket gopher (*Thomomys* spp.) management (Proulx 1997, Baldwin et al. 2016). Typically, the best way to minimize damaging rodent populations is to develop an Integrated Pest Management (IPM) program that utilizes a combination of techniques to maximize efficacy (Engeman and Witmer 2000). Adherence to an IPM program also requires consideration of the impact that control techniques might have on the environment. Currently, there is a strong push to limit the use of rodenticides to minimize the negative impacts, real or perceived, that they can have on non-target species (see Baldwin and Salmon (2011) for discussion). However, rodenticides are typically highly efficacious and cost effective (Messmer and Schroeder 1996, Baldwin et al. 2014, Baldwin et al. 2017), so alternative management tools need to be similarly successful.

Pocket gophers and voles (*Microtus* spp.) cause significant damage to numerous agricultural crops in the American West (e.g. gophers: (Miller 1953, Howard and Childs 1959, Luce et al. 1981, Askham 1988, Marsh 1994, Smallwood and Geng 1997, Baldwin et al. 2014); voles: (Askham 1988, Witmer et al. 2009, Baldwin et al. 2014). Because pocket gophers are a fossorial rodent that primarily consume the fleshy taproots of plants, their populations are highly responsive to vegetation cover and types (Sullivan and Hogue 1987). Pocket gopher burrows can also threaten earthen levee systems (Ordeñana et al. 2012), spread weeds (Cook 1939), and damage subsurface drip irrigation systems (Montazar et al. 2017). Voles forage on

both the underground and aboveground biomass of plants, and can kill plants by girdling their trunks, or cause sub-lethal damage leading to reduced growth and yields (Byers 1984, Clark 1984, Merwin et al. 1999). Vole populations commonly undergo eruptive fluctuations every few years as a result of food availability, environmental stochasticity, and possibly predator densities (Chitty and Phipps 1966, Krebs 1966, Boonstra 1977, Beacham 1979). Pocket gophers spend the majority of their lives in extensive burrow systems; voles utilize both underground burrow systems and forage above ground, often creating well-worn runways through vegetation. While both pocket gophers and voles cause significant damage in agricultural fields, pocket gophers are considered ecosystem engineers in natural systems, where their burrowing and foraging activity can change soil structure, alter aboveground biomass, and prevent tree establishment and succession in grasslands (Miller 1957, Reichman and Smith 1985, Cantor and Whitham 1989, Jenkins and Bollinger 1989). Pocket gophers and voles are also an important component of natural food webs, and vacated pocket gopher burrows are used by several species of conservation concern (Smallwood et al. 2001).

Whether predators are capable of controlling or reducing populations of herbivorous prey has been a longstanding debate in ecology (Krebs et al. 2001). For example, in naturally cycling populations of herbivorous mammals at high latitudes, numerous studies have attempted to elucidate whether predators play a role in population increases or declines (Boonstra 1977, Beacham 1979, Baker and Brooks 1982, Korpimaki and Krebs 1996, Reid et al. 1997, Therrien et al. 2014). One common argument against any predators' ability to control a prey population is derived from the theory that predators kill weak individuals that can be quickly replaced through increased breeding success of surviving individuals, known as compensatory mortality (Errington 1963). In natural systems, experimentally manipulating predator numbers has had both significant and nonsignificant effects on prey populations (Holt et al. 2008, Salo et al. 2010), with many experiments focused on the removal of predators or the impacts of introduced predators. Agricultural systems, however, differ greatly from most natural habitats because they are often irrigated, have high concentrations of food resources, and are often low in predator abundance because of a lack of viable habitat. By reintroducing

or artificially inflating native predator densities in agriculture, it may be possible to create or increase top-down pressure on herbivorous prey populations.

Barn owls (*Tyto alba*), historically lauded by farmers for their voracious appetites and cosmopolitan life histories (Fisher 1893), are again catching the eye of farmers in many regions around the world as a potential natural method for small mammal control. Barn owls are an appealing method for controlling small mammal pests because they are relatively cheap to establish, have relatively low maintenance costs, are less territorial than most other predators, and are highly effective predators of certain rodents, such as pocket gophers or voles (Browning et al. 2016). Despite a multitude of studies documenting barn owl consumption of rodent pests there have been relatively few field studies that have quantified the barn owl's ability to reduce or control populations of small rodents in agricultural regions (but see, Duckett and Karuppiah 1990, Chia et al. 1995, Ho and Teh 1997, Ojwang and Oguge 2003, Browning et al. 2016) and this lack of data has prompted criticism of programs that claim that owls provide such services (Marsh 1998, Moore et al. 1998, Schmidt 2003, Wood and Fee 2003). This discrepancy between the popularity of installing barn owl boxes and lack of field data confirming the ability of owls to control rodent pests is perhaps most stark in California, where numerous studies (Clark and Wise 1974, Van Vuren et al. 1998, Kross et al. 2016) have documented the diet of owls, but no field studies have simultaneously collected data on owls and the populations of main rodent pests of crops in the area (but see Browning et al. 2016 for an experiment that monitored gopher mounds). This is likely because the main mammalian pests of most crops in California spend the majority of their time in underground burrows (Baker et al. 2003, Pugh et al. 2003) and are therefore harder to monitor than the arboreal and terrestrial species for which barn owls have been shown to be effective (Duckett and Karuppiah 1990, Chia et al. 1995, Ho and Teh 1997, Ojwang and Oguge 2003, Browning et al. 2016).

Despite our understanding of the damage associated with pocket gopher and vole populations, as well as the popular use of barn owls as a biocontrol, there has been little research focused on how well barn owls control rodent populations. Model simulations are a way to approximate the efficacy of barn owls as a biocontrol for pest rodent populations. Population models have been used to understand and predict how multiple scenarios affect a

target population. For example, models have been used to understand the role of parasites in controlling host populations (Deter et al. 2008), to determine the effects of introduced species on the demographics of native species (Stapp and Hayward 2002), and to predict how different management strategies will affect populations of rodent pests (Stenseth et al. 2001).

Population models are best used once enough field data is available to accurately inform model parameterization and are often much more simplistic than actual biological patterns (Korpimäki and Krebs 1996). However, population models can be powerful tools for understanding the scenarios under which population trends are likely to occur, and can help field biologists understand the most important variables to collect and experimentally manipulate to understand natural predator-prey processes. Here, we present the results of a combined demographic model and predator-prey model simulation based on data for barn owl diet, and on rodent breeding-, survival-, and mortality-rates extracted from the scientific literature. We sought to estimate at which densities barn owls would need to be present on a farm to control each prey species under varying prey carrying capacities and population growth rates. These models provide a framework to better understand the potential for barn owls to control rodent pests.

METHODS

Predator-Prey Models

We adapted the Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963), to explore the interactions between predator and prey species. The original model, which applies to a specialist predator, comprises two differential equations describing the dynamics of the prey (N) and predator (P):

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K_{prey}} \right) - \frac{k_{max}N}{N+D} P \quad (\text{eq. 1})$$

$$\frac{dP}{dt} = \beta PN - \delta P \quad (\text{eq. 2})$$

(see Table 1 for parameter definitions). Eq. (2) shows that the predator abundance is regulated by the focal prey species abundance, and that the predator population will decline if the focal prey species abundance is too low. We assume that the owls can switch to alternative prey when the focal species is at low abundance, and that the alternative prey are abundant enough that the owl population is limited by the number of nest boxes on the landscape (controlled by the manager). Therefore, we modify the model to hold the density of owls constant for each respective model. This is represented by equation 3, where the predator density does not change:

$$\frac{dP}{dt} = 0; \quad (\text{eq. 3})$$

P is then constant with a value set by the manager.

We did not include predation as a pulsed treatment, but rather as a continuous effect on an existing pest population. This modeling approach allowed us to simulate the impacts of a pest-control program with different densities of barn owls for both pocket gopher and vole species, separately. We also varied the population growth rate, initial population size, and carrying capacity of each prey species to determine their impacts on barn owls as a biocontrol. By varying these parameters, we are able to gain insights into how control by barn owls might vary in different landscapes. We were specifically interested in the population density that the

pocket gopher and vole populations could be driven to in the presence of barn owls. Equations 1 and 2 show the relationship between the change in prey and predator populations. For Equation 1, we used a Holling type-II functional response to define the predation rate.

Table 1: State Variables and Parameters used in Predator Prey Models.

State Variable	Definition	Value	Source
N	Prey density (prey abundance/ha)	Varied in simulation, see Table 4	Set in simulation
P	Predator density (barn owls/ha)	Varied in simulation, see Table 4	Set in simulation
Parameter	Definition		
r	Population growth rate of prey (pocket gopher or vole) population (prey individuals/season)	Varied in simulation, see Table 4	Calculated from literature values
K_{prey}	Carrying capacity of the prey population (prey abundance/ha)	Varied in simulation, see Table 4	Set in simulation
k_{max}	Maximum feeding rate of the barn owls on prey populations (prey individuals/season)	654 for voles 378 for pocket gophers	Calculated from empirical data (Kross and Baldwin 2016)
D	Half saturation constant ($1/\alpha h$), abundance of prey at which the barn owl feeding rate is half the maximum (prey abundance/ha)	990	Derived from Derting and Cranford (1989)
α	Attack rate or capture efficiency of the barn owl (per season)	0.92	From Derting and Cranford (1989)
β	Assimilation efficiency of the barn owl (unitless)	5.85e-4 for voles 1.01e-3 for pocket gophers	Derived from data described in this report
δ	Death rate of the barn owl pair (barn owls/season)	0.01	From Bunn et al. (1982)
h	Handling time: the proportion of time it takes an owl to consume a single prey item ($1/k_{max}$) (season/prey item)	1.52e-3 for voles, 2.65e-3 for	Calculated from empirical data in (Kross and Baldwin

pocket
gophers

2016)

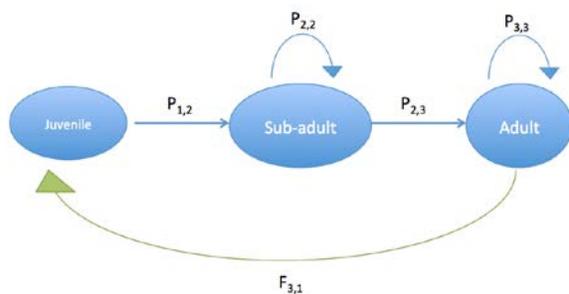
To calculate the diet of an average nesting pair of barn owls and their progeny (hereafter: a barn owl nest), we used field data collected from pellet- and video- based barn owl diet studies (Van Vuren et al. 1998, Browning et al. 2016, Kross and Baldwin 2016, Kross et al. 2016) in agricultural lands in California. This allowed us to estimate the weekly required biomass of a barn owl nest, as well as seasonal changes in prey choice (see Kross and Baldwin 2016 for additional details). We used prey-delivery rates (Browning et al. 2016) and seasonal dietary composition (Van Vuren et al. 1998) to determine that a single adult owl would require 68.70kg of prey to feed itself and five chicks (nest average in our targeted study area is 4.33 chicks; (Browning et al. 2016). Using dietary composition data from Kross et al. (2016) and Van Vuren et al. (1998), we calculated that the average size of a pocket gopher caught by barn owls was 64.72g, and the average size of a vole was 37.36g. We then estimated the assimilation efficiency for barn owls (β) by calculating the relative biomass proportion of one pocket gopher prey item (1.01×10^{-3}) or one vole prey item (5.85×10^{-4}) toward the requirement for raising one chick in a nest that averaged 4.33 barn owl chicks. K_{\max} was calculated by assuming the number of prey individuals required to support a nest of five barn owl chicks was the maximum number of prey captured per season.

Population Matrices

We created stage-structured population matrices (Figure 1) for both pocket gophers and voles using data extracted from the literature. Stage-structured population matrices predict population growth for species with multiple distinct age-based stages by taking into account the probability that an individual within a given age class (or stage) will survive or move into the next stage, and whether each individual will produce offspring within a given time step. Individual animals 'enter' a given stage at the start of a time step and by the next time step they will either move into the next stage, remain within the same stage, or die. Individuals may also reproduce within the time step, and new offspring are added to the lowest stage structure.

Since our predator-prey models utilized 3-month long seasonal time steps, we scaled all demographic data to the same seasonal timing.

We used female vole and pocket gopher data from the literature to construct population matrices. For these matrices, minimum and maximum survival and fertility rates were identified from the literature for each stage of the pocket gopher and vole life cycle. Gopher stage structures were described in three stages: juvenile, sub-adult, and adult stages (Figure 1). For pocket gophers, the appropriate stage-structure classifications are based on maternal care, pelage, and reproductive status. Juvenile pocket gophers are still under maternal care and do not leave their maternal burrow system where they remain for 35-45 days prior to weaning (Howard and Childs 1959), sub-adult pocket gophers have left their maternal burrow systems but are smaller than fully-grown adult females and have a pubic symphysis gap of <6mm so have not yet reproduced, and adult pocket gophers are sexually mature and have a fully dissolved pubic symphysis gap >6mm (Loeb 1990). The length of time that pocket gophers spend in sub-adult stages prior to breeding depends on when they are born, with individuals born early in the spring potentially breeding in their first year, and those born in summer or fall generally waiting until the following spring to breed, although breeding can occur year-round in some areas and habitats (e.g. Miller 1946, Loeb 1990), but generally is once females are 7 months old (Daly and Patton 1986).



	Juvenile	Sub Adult	Adult
Juvenile	0	0	$F_{3,1} * P_{3,3}$
Sub Adult	$P_{1,2}$	0	0
Adult	0	$P_{2,3}$	$P_{3,3}$

Figure 1: Population matrix structure used for prey models.

$P_{1,2}$: probability a juvenile will survive and become a sub-adult

$P_{2,2}$: probability a sub-adult will survive and remain a sub-adult (assumed to be zero because all subadults advance to the adult stage)

$P_{3,2}$: probability an adult will revert to the subadult stage (zero because individuals cannot regress classes)

$P_{1,3}$: probability an adult will revert to the juvenile stage (zero because juveniles must pass through the subadult stage)

$P_{2,3}$: probability a sub-adult will survive and become an adult

$P_{3,3}$: probability an adult will survive and remain an adult

$F_{1,1}$: Fecundity of juveniles (assumed to be zero)

$F_{3,1}$: Fecundity of adults

For voles, stage is classified based on age and pelage. Voles are classified as juvenile from birth to approximately 3 weeks of age, sub-adult from 3 weeks to 8-9 weeks, and adults thereafter (Cudworth and Koprowski 2010). Because of the rapid transition from juvenile to subadult, only two stages were represented in the matrix models – juvenile and adult, with juveniles reproducing at the end of their stage transition (Figure 2).

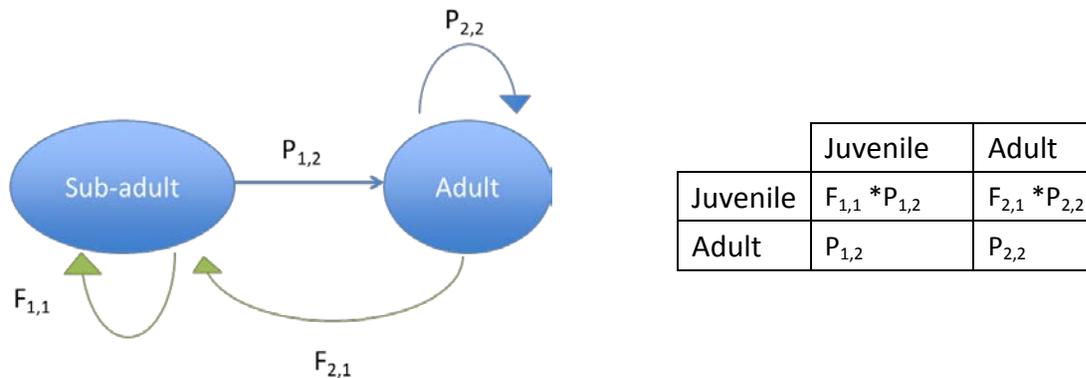


Figure 2: Population matrix structure used for prey models.
 $P_{1,2}$: probability a juvenile will survive and become an adult
 $P_{2,2}$: probability an adult will survive and remain an adult
 $F_{1,1}$: Fecundity of juveniles
 $F_{2,1}$: Fecundity of adults

Population matrices were constructed using the minimum, maximum, and average values found in the literature, for both species (Tables 2 & 3). There are no data in the literature on the survival rates of juvenile pocket gophers, most likely because juveniles do not leave their maternal burrows and are therefore rarely caught during field studies. Therefore, we have used a value of 0.5, which is the same as vole survival in the juvenile stage. Vole demographic data were extracted in the same way, but it is important to note that survival measurements include some from *M. townsendii* in addition to measurements from *M. californicus* to include more studies from agricultural habitats. Because this study was exploratory in nature, this provides a good first approximation for how we might expect vole populations to grow over time.

Table 2: Stage-structured matrices used for pocket gophers showing probability that an individual within each stage will survive and move to the next stage and the fecundity (number of offspring) that an individual of each stage will produce within a time step. Models based on minimum, mean, and maximum values found in the literature are shown side by side. See Figure 1 for an explanation of stage-structured models and which probabilities are represented in each cell of the tables.

¹Loeb 1990, ²Anderson & MacMahon 1981, ³Howard & Childs 1959, ⁴Daly & Patton 1986

Age Stage	Minimum			Mean			Maximum		
	Juvenile	Sub Adult	Adult	Juvenile	Sub Adult	Adult	Juvenile	Sub Adult	Adult
Juvenile	0	0	1.688 ¹	0	0	2.968	0	0	4.463 ¹ *0.833 ²
Sub Adult	0.5	0	0	0.5	0	0	0.5	0	0
Adult	0	0.658 ²	0.746 ⁴	0	0.765	0.799	0	0.872 ³	0.833 ²

Table 3: Population matrices used for voles showing probability that an individual within each stage will survive and move to the next stage and the fecundity (number of offspring) that an individual of each stage will produce within a time step. Minimum, mean, and maximum values are shown side by side. See Figure 1 for an explanation of stage-structured models and which probabilities are represented in each cell of the tables. ¹Beacham 1979, ²Krebs 1966, ³Boonstra & Krebs 1976, ⁴Beacham 1979a, ⁵Boonstra 1977a, ⁶Krohne 1980, ⁷Hoffman 1958, ⁸Batzli & Pitelka 1971

Age Stage	Minimum		Mean		Maximum	
	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult
Juvenile	3.456 ⁶ *0.20	3.456 ⁶ *0.02	5.02*0.28	5.02*0.35	6.56 ⁷ *0.41	6.56 ⁷ *0.51
Adult	0.20 ²	0.02 ¹	0.28	0.35	0.41 ⁸	0.51 ⁸

For both pocket gophers and voles, the instantaneous rate of population growth (r) was calculated by first calculating the geometric population growth rate (λ) from the stage structured matrices using the popbio package in R (Stubben and Milligan 2007). The popbio package calculates λ by identifying the dominant eigenvalue in a population matrix. From λ , we can calculate the parameter r , using the approximation $r = \log_e(\lambda)$. This conversion allows us to move from a structured (matrix) to an unstructured (logistic growth) model, but it requires the assumption that there are no time lags associated with growth and that the matrices are derived from measurements taken when the population is not experiencing density dependence. Thus, the estimates of r should be viewed as rough approximations of possible growth rates for both pocket gopher and vole populations might be.

Because of the unique life cycle of vole populations, r was calculated using a 10 week time step in the matrix models, approximating five generations per year. The r was then adjusted to reflect a seasonal growth rate (approximately 13 weeks) for consistency of a seasonal time step in the predator-prey models. For both vole and gopher populations, the minimum calculated growth rate was negative ($r=-0.43$ and -0.21 , respectively). Because this report is particularly interested in pests which have a positive growth rate, a minimum r -value of 0.01 was chosen to represent very low (but still positive) growth in the vole and pocket gopher populations.

Simulations

Simulations were run over a period of 20 seasonal (3-month) time steps for pocket gophers and voles (5 years total), with all analyses conducted in R v. 3.4.0 (R Core Development Team 2017). Simulations were run for these relatively short periods of time to focus on outcomes in a management-relevant time scale. Initial population densities of prey and barn owl populations were varied along with parameter values for population growth rate (r) and prey carrying capacity (K). Table 4 shows the range of N , P , r , and K values used in simulations. For reference, Table 4 also includes calculated annual r -values.

Table 4: Range of state variables that were used in model simulations.

Parameter or State Variable	Range
$N_{\text{pocket gopher}}$	175, 100, 50, 10, 2
N_{vole}	1000, 500, 10, 05, 10, 2
P	0.2, 0.6, 1.0, 2.0
$K_{\text{pocket gopher}}$	175, 100, 50, 25
K_{vole}	1000, 500, 100, 50
$r_{\text{pocket gopher}}$	0.35, 0.51, 0.65
$r_{\text{pocket gopherAnnual}}$	0.04, 1.12, 1.68
r_{vole}	0.01, 0.70, 1.45
$r_{\text{voleAnnual}}$	0.04, 2.8, 5.8

RESULTS

Predator Prey Models

Pocket Gopher Simulations

Under all simulations, the presence of barn owls resulted in pocket gopher populations remaining below the environmental carrying capacity at the end of 5 years. At the two highest barn owl densities (1 and 2 pairs per ha), pocket gopher populations were always driven to extinction (Figures 3-6). This was usually achieved by about the middle of the second year at the highest barn owl density (2 pairs per ha). At moderate barn owl densities of 0.6 pairs per ha, pocket gophers were driven to zero at the low and moderate r -values ($r = 0.01$ and 0.28 , respectively), but not within the 5-year time scale at maximum r -values (Figures 3-6). At the lowest barn owl densities (0.2 pairs per ha), pocket gopher populations were never driven to zero in the time period examined, regardless of the growth rate or carrying capacity values used. At the lowest barn owl densities, under moderate ($r=0.28$) and high ($r=0.42$) population growth rates those populations rose to an equilibrium at approximately 45% and 65% of K , respectively (Figures 3-6, panels b and c).

In situations where gopher populations were equal to carrying capacity at the initiation of barn owl predation efforts, all densities of barn owls led to some reduction of gopher populations ranging from 65% of carrying capacity (barn owl density of 0.2, gopher population growth rate of 0.42), to extinction of gopher populations (Figures 3-6, panel a). In areas where initial pocket gopher populations were intermediate (approximately 0.5 K ; potentially due to existent management efforts), barn owl predation led to a reduction in gopher population densities under all scenarios except when barn owls were at their lowest densities and pocket gopher population growth rates were at their highest (Figure 7). In areas where initial pocket gopher populations were 2 (a potential reinvasion scenario), only at very low barn owl densities (0.2 pairs/ha) did pocket gopher populations grow to reach an equilibrium at approximately 50% of K within five years (Figure 8). At all other barn owl densities, pocket gopher populations under the reinvasion scenario shrunk to zero within the five year timeframe (Figure 8).

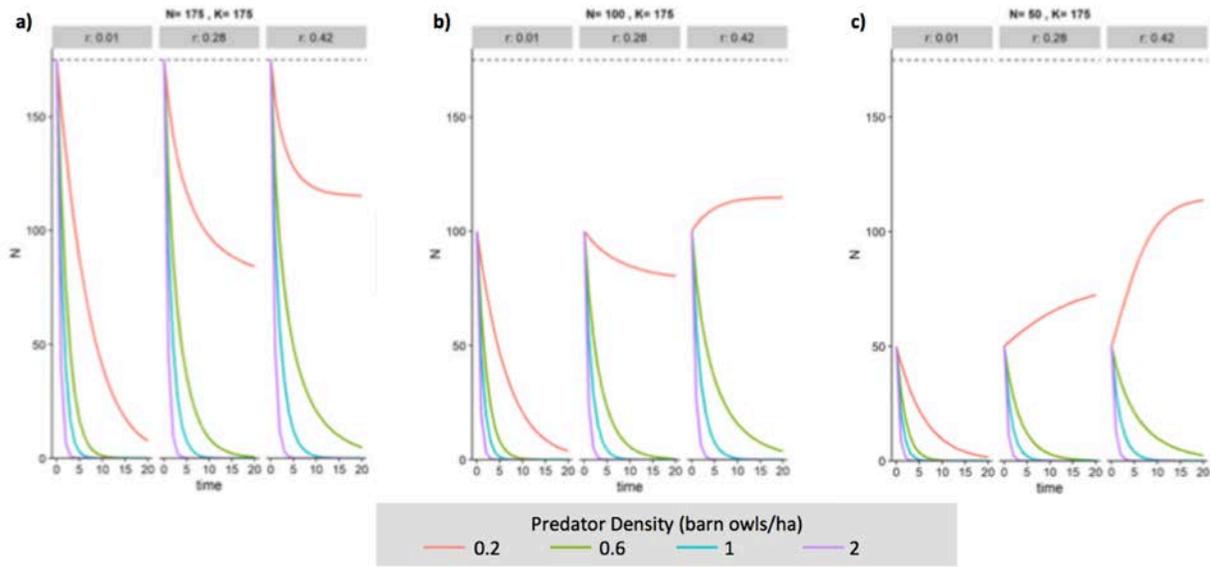


Figure 3: The effects of varying predator densities (barn owls/ha), starting pocket gopher densities ($a=175, b=100, c=50$) and pocket gopher population growth rate (r -values, shown in grey bars above graphs) on a population of pocket gophers with a carrying capacity (K) of 175 pocket gophers/ha (dashed horizontal line). Each time step represents one 3-month season.

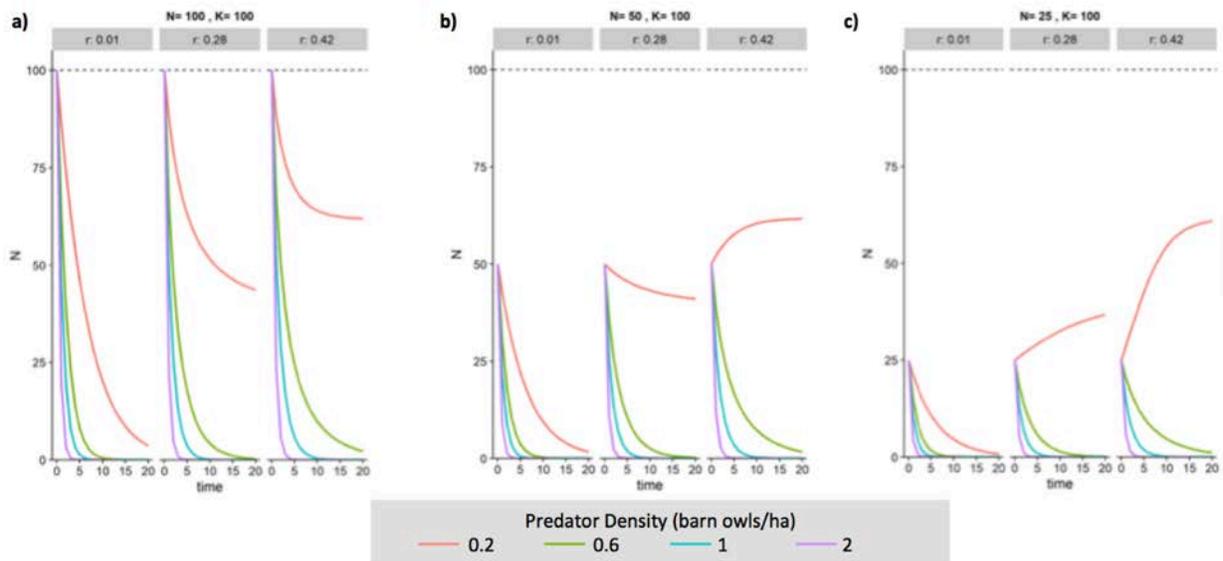


Figure 4: The effects of varying predator densities (barn owls/ha), starting pocket gopher densities ($a=100, b=50, c=25$) and pocket gopher population growth rate (r -values, shown in grey bars above graphs) on a population of pocket gophers with a carrying capacity (K) of 100 pocket gophers/ha (dashed horizontal line). Each time step represents one 3-month season.

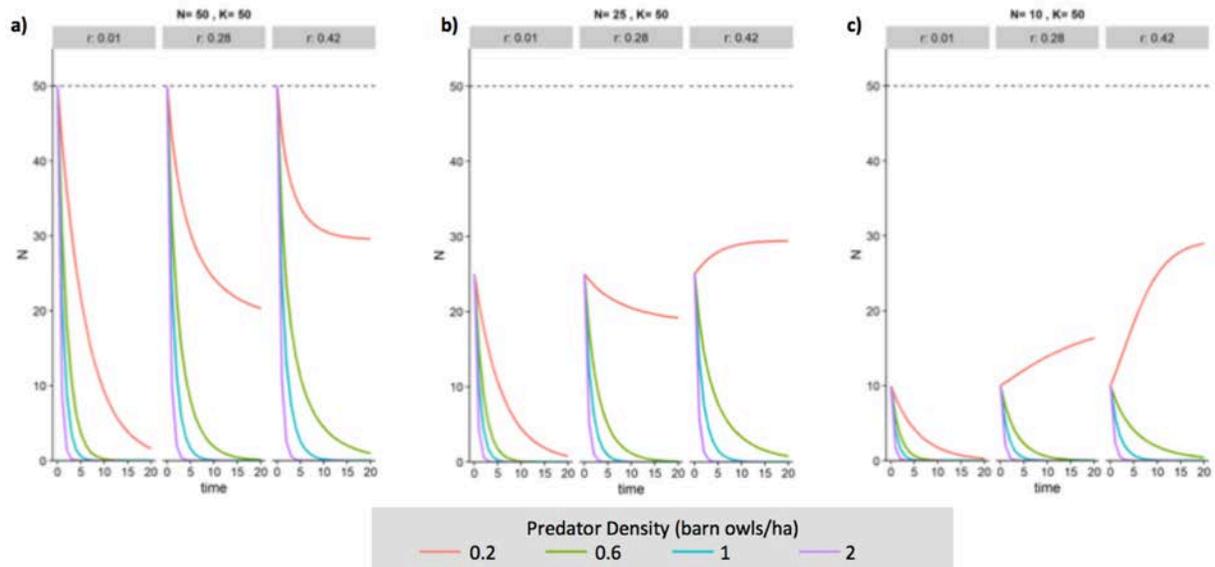


Figure 5: The effects of varying predator densities (barn owls/ha), starting pocket gopher densities ($a = 50, b = 25, c = 10$) and pocket gopher population growth rate (r -values, shown in grey bars above graphs) on a population of pocket gophers with a carrying capacity (K) of 50 pocket gophers/ha (dashed horizontal line). Each time step represents one 3-month season.

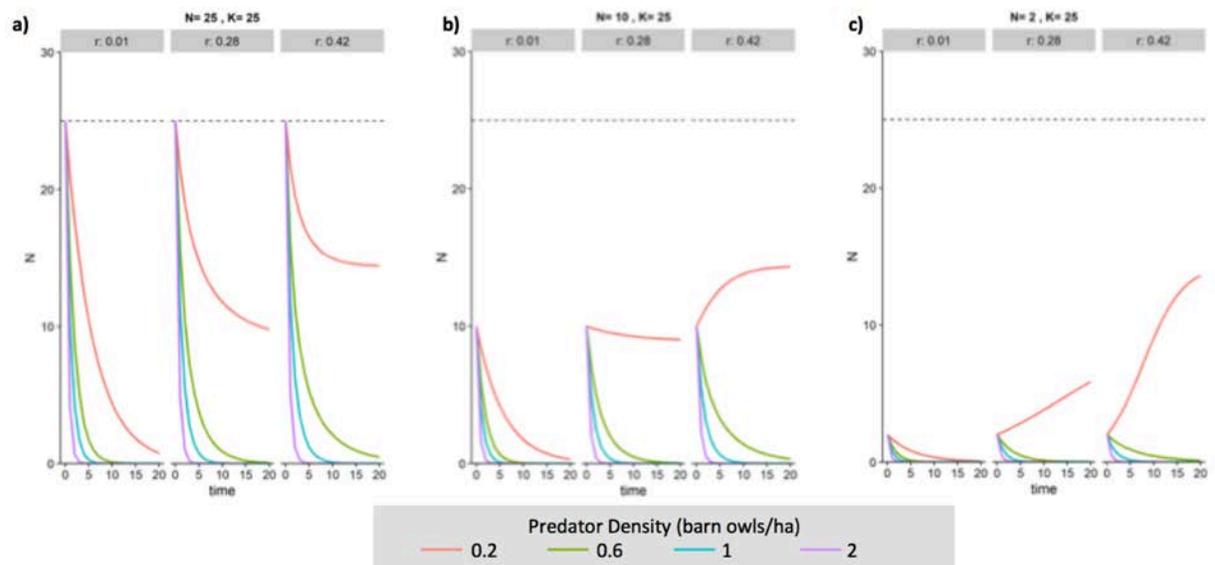


Figure 6: The effects of varying predator densities (barn owls/ha), starting pocket gopher densities ($a = 25, b = 10, c = 2$) and pocket gopher population growth rate (r -values, shown in grey bars above graphs) on a population of pocket gophers with a carrying capacity (K) of 25 pocket gophers/ha (dashed horizontal line). Each time step represents one 3-month season.

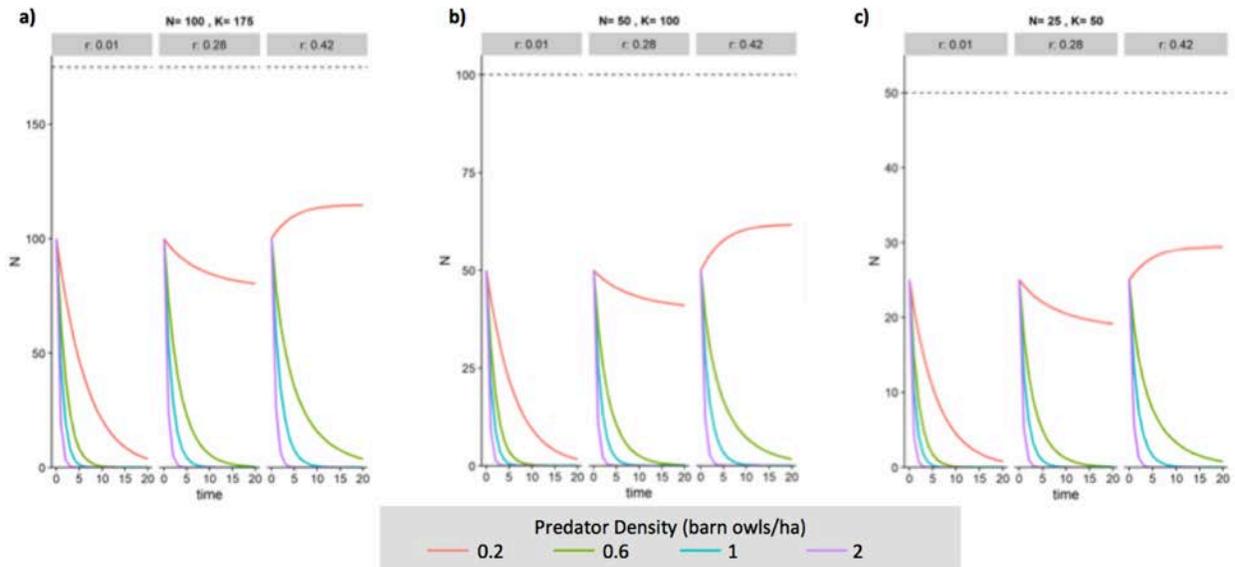


Figure 7: The effects of varying predator densities (barn owls/ha) on pocket gopher populations that start at a density that is approximately half of the environmental carrying capacity (K, shown as dashed horizontal line). Each panel depicts 3 graphs of different pocket gopher population growth rate (r-values, shown in grey bars above graphs). Each time step represents one 3-month season.

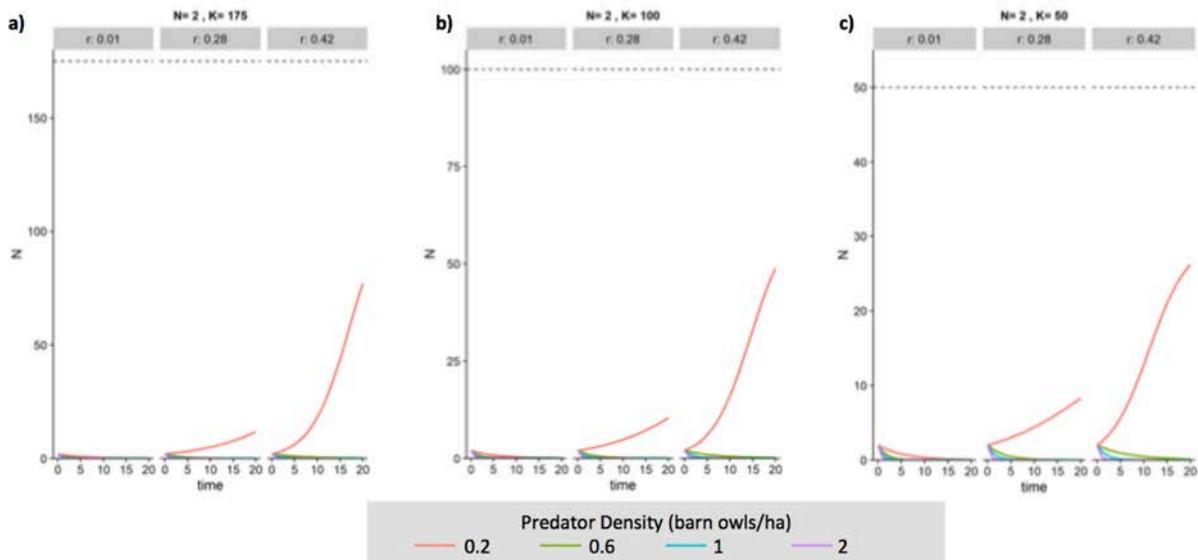


Figure 8: The effects of varying predator densities (barn owls/ha) and pocket gopher carrying capacities (K, dashed horizontal line) on gopher populations that start at $N=2$, representing a potential situation where pocket gophers invade a new area. Each panel depicts 3 graphs of different pocket gopher population growth rates (r-values, shown in grey bars above graphs). Each time step represents one 3-month season.

Vole Simulations

Under all simulations, the presence of barn owls resulted in vole populations remaining below the environmental carrying capacity at the end of 5 years (Figures 9-12). At high barn owl densities (1 and 2 pairs/ha), barn owls were able to drive vole populations to extinction at low and moderate vole population growth rates. Only at the highest barn owl densities (2 pairs/ha) were barn owls able to drive vole populations to extinction when vole population growth rates were high (Figures 9-12). At moderate barn owl population densities (0.6 pairs/ha), owls were able to drive vole populations to extinction at very low vole population growth rates ($r=0.01$), were able to drive vole populations to approximately 3-55% of K at moderate vole population growth rates ($r=0.7$), and were able to drive vole populations to approximately 63-83% of K at high vole population growth rates ($r=1.45$). At the lowest barn owl densities (0.2 pairs/ha), owls were able to drive vole populations toward extinction at very low vole population growth rates ($r=0.01$) only when the initial vole population was 2, and kept vole populations at below 10% of the carrying capacity at other initial vole populations (Figures 9-12). At their lowest densities, barn owls were able to drive vole populations to 75-88% of K at moderate vole population growth rates ($r=0.7$; Figures 9-12), and were able to drive vole populations to 88-95% of K at high vole population growth rates ($r=1.45$).

In situations where vole populations were equal to carrying capacity at the initiation of barn owl predation efforts, all densities of barn owls led to some reduction of vole populations ranging from 94.5% of carrying capacity (barn owl density of 0.2, vole population growth rate of 1.45), to extinction of vole populations, depending on owl densities and vole population growth rates (Figures 9-12, panel a). In areas where initial vole populations were intermediate (approximately 20-50% of K ; potentially due to existent management efforts) barn owl predation led to a further reduction in populations under some scenarios (Figure 13). In areas where initial vole populations were 2 (a potential reinvasion scenario), vole populations either shrunk to zero or rose to an equilibrium below the environmental carrying capacity depending on barn owl densities and vole population growth rates (Figure 14).

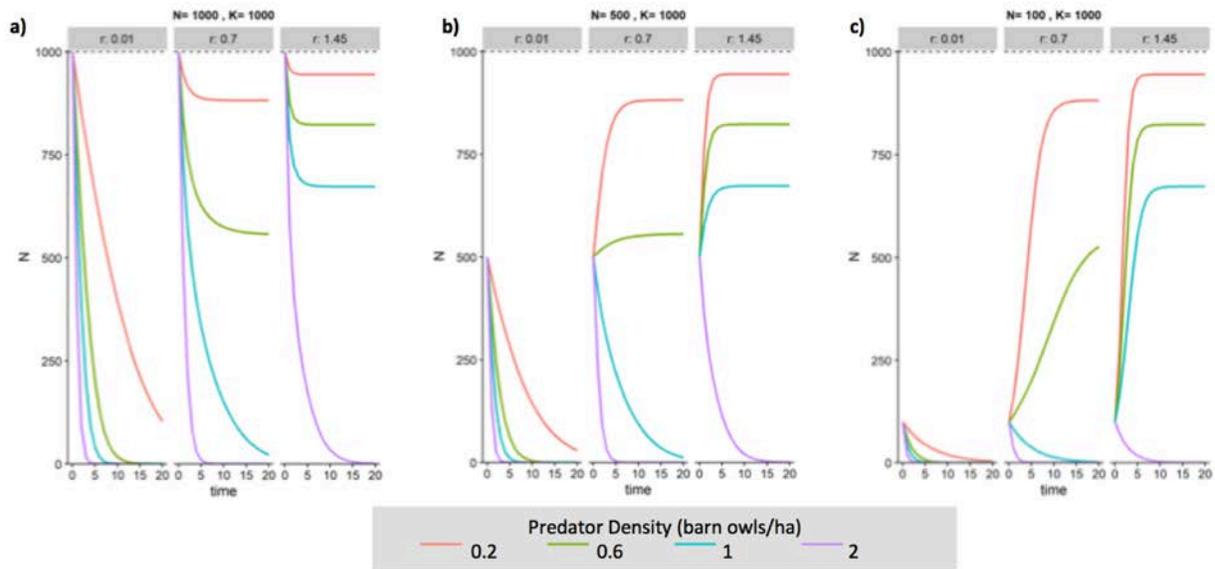


Figure 9: The effects of varying predator densities (barn owls/ha), starting vole densities ($a=1000, b=500, c=100$) and vole population growth rate (r -values, shown in grey bars above graphs) on a population of voles with a carrying capacity (K) of 1000 voles/ha (dashed horizontal line). Each time step represents one 3-month season.

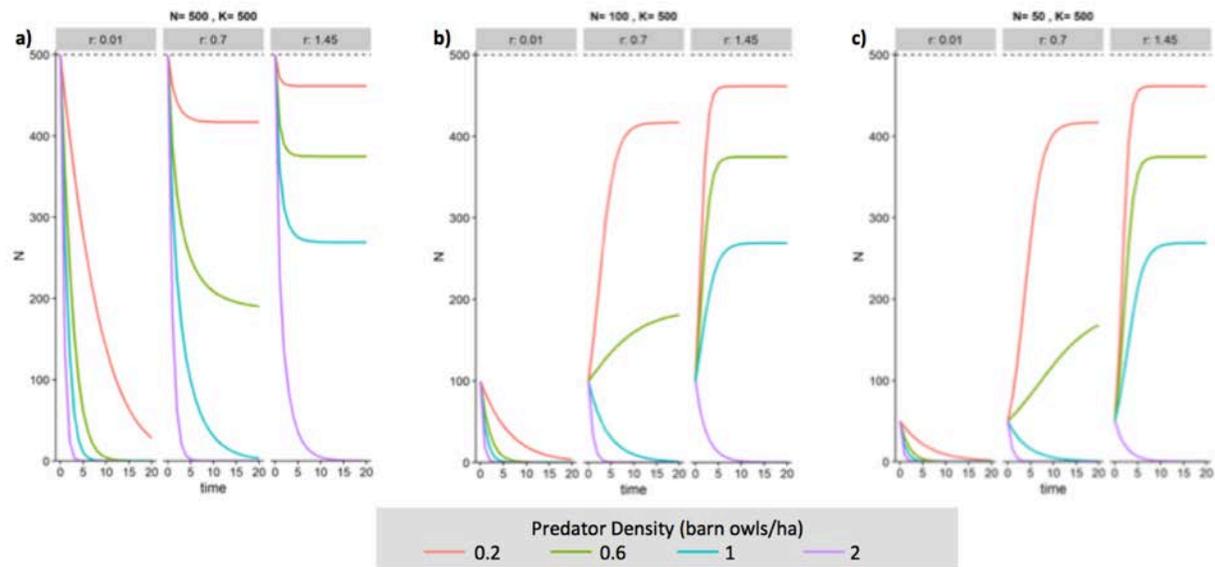


Figure 10: The effects of varying predator densities (barn owls/ha), starting vole densities ($a=500, b=100, c=50, d=50$) and vole population growth rate (r -values, shown in grey bars above graphs) on a population of voles with a carrying capacity (K) of 500 voles/ha (dashed horizontal line). Each time step represents one 3-month season.

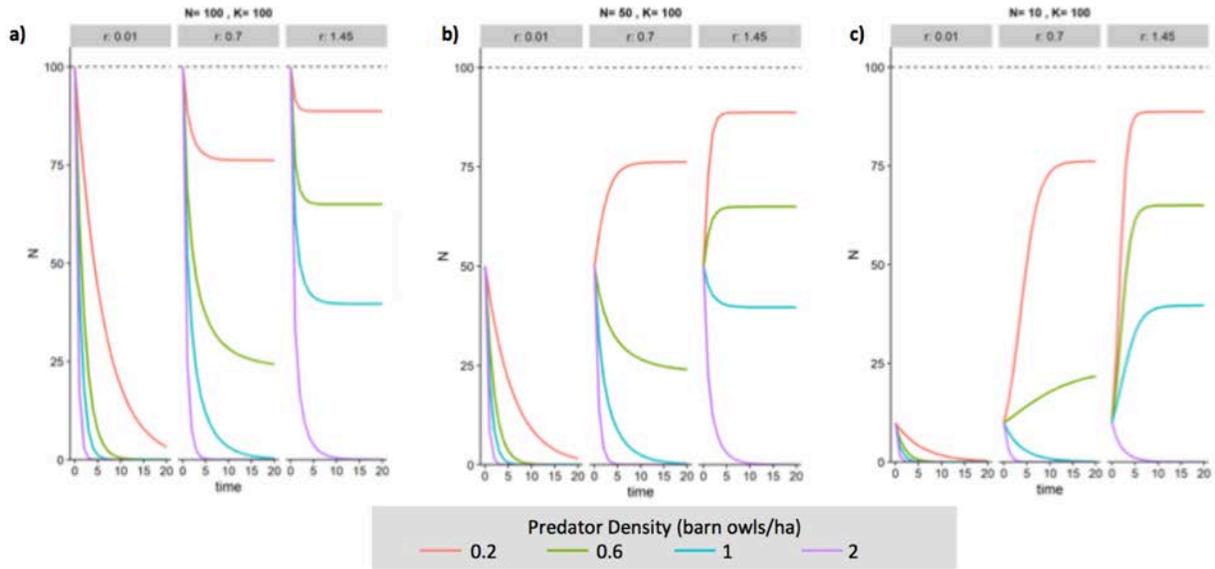


Figure 11: The effects of varying predator densities (barn owls/ha), starting vole densities ($a=100$, $b=50$, $c=10$) and vole population growth rate (r -values, shown in grey bars above graphs) on a population of voles with a carrying capacity (K) of 100 voles/ha (dashed horizontal line). Each time step represents one 3-month season.

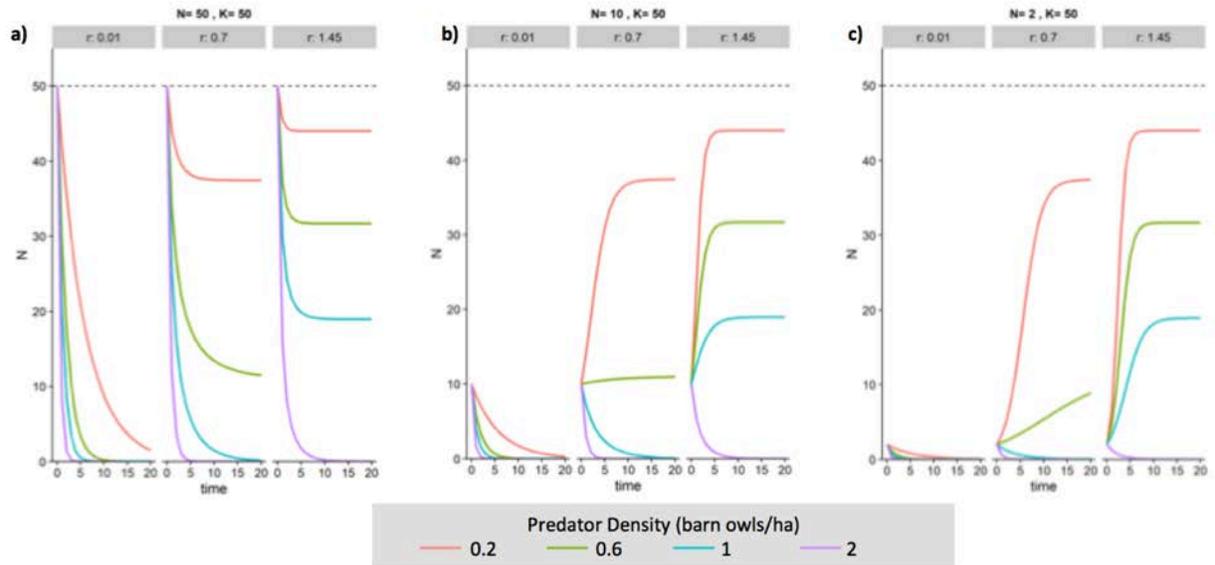


Figure 12: The effects of varying predator densities (barn owls/ha), starting vole densities ($a=50$, $b=10$, $c=2$) and vole population growth rate (r -values, shown in grey bars above graphs) on a population of voles with a carrying capacity (K) of 50 voles/ha (dashed horizontal line). Each time step represents one 3-month season.

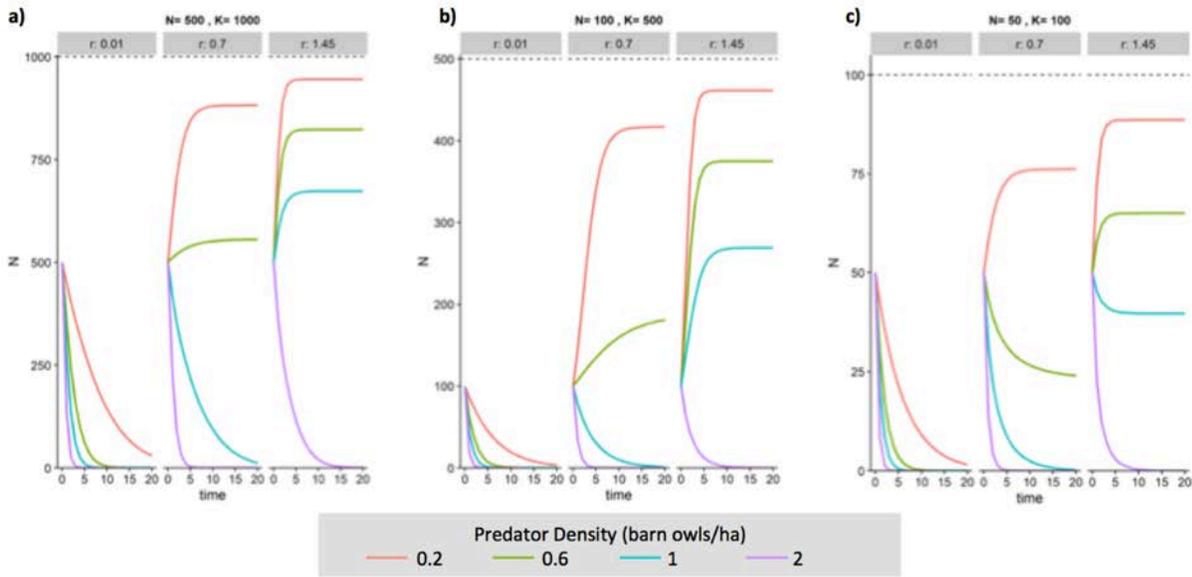


Figure 13: The effects of varying predator densities (barn owls/ha) on vole populations that start at a density that is 20% to 50% of the environmental carrying capacity (K , shown as dashed horizontal line) representing a potential situation where growers are controlling voles using traditional methods such as trapping. Each panel depicts 3 graphs of different vole population growth rate (r -values, shown in grey bars above graphs). Each time step represents one 3-month season.

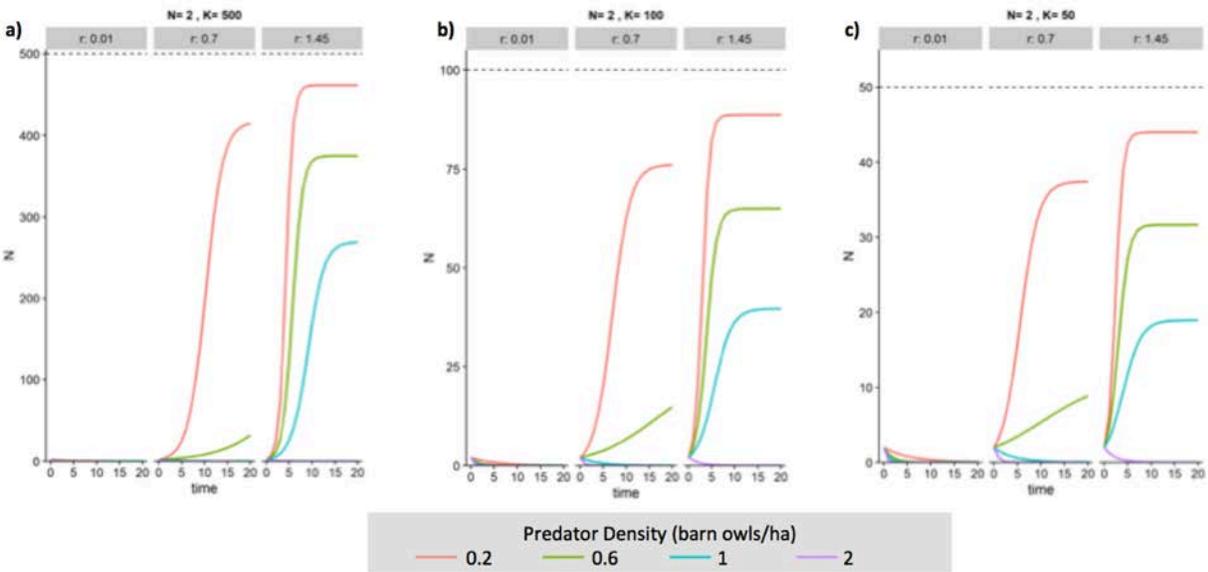


Figure 14: The effects of varying predator densities (barn owls/ha) and vole carrying capacities (K , dashed horizontal line) on vole populations that start at 2, representing a potential situation where voles invade a new area. Each panel depicts 3 graphs of different vole population growth rate (r -values, shown in grey bars above graphs). Each time step represents one 3-month season.

DISCUSSION

Our models indicate that barn owls are capable of reducing the densities of pocket gophers and voles, and that under all scenarios owl predation drives the populations of these rodents below the environmental carrying capacity. These results are hopeful for the utility of barn owls as a component of an IPM program to control rodent pests, but field studies to better understand the effects of owls on prey populations under different conditions are essential, especially given the inability of our models to incorporate the many complex factors that affect owls, rodents, and farmer income (Figure 15).

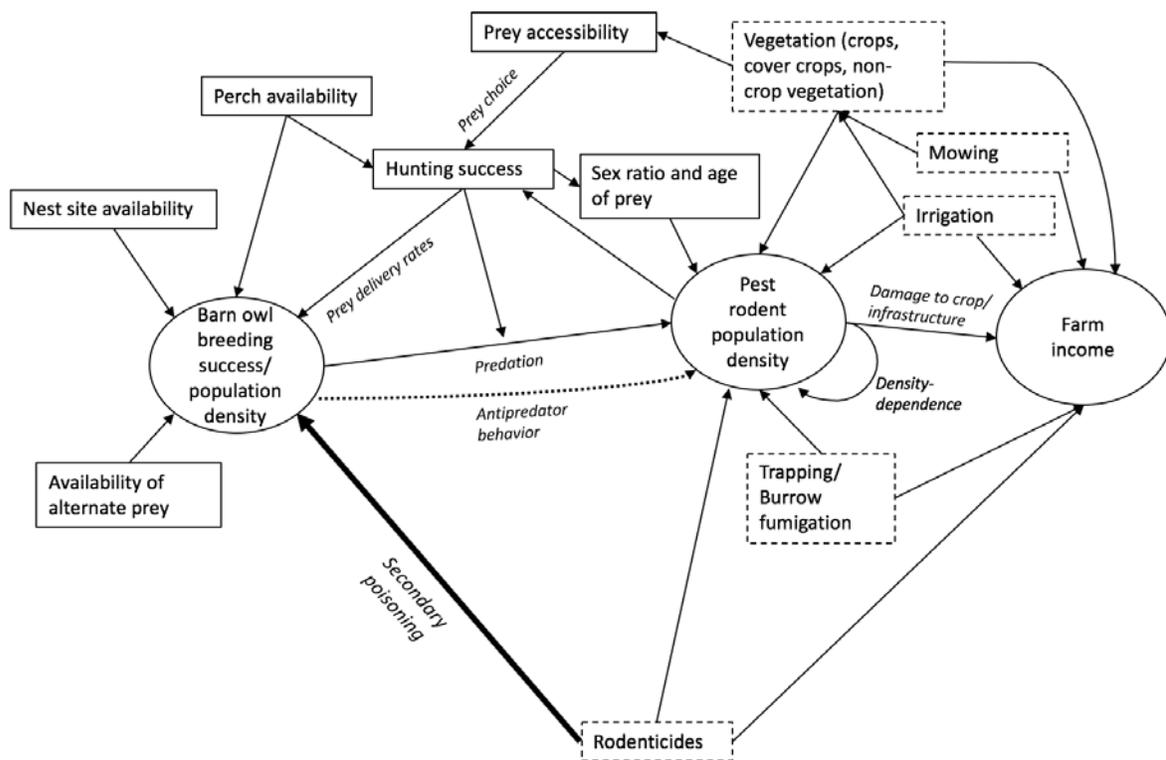


Figure 15: Conceptual model of the factors affecting the efficacy of barn owl control of rodent pests on farms. Boxes with dashed lines indicate farm management practices, arrows represent processes and effects that boxes have on each other. Establishment and cleaning of barn owl nest boxes will also affect farm income.

At moderate to high owl densities, our models indicate that barn owls have the potential to reduce, perhaps substantially, pocket gopher populations. Therefore, if the

carrying capacity of the landscape is low, then barn owls may be effective at driving down pocket gopher populations to a manageable level. Compared to voles, pocket gophers reproduce more slowly so management through barn owls may be more effective.

For voles, our models indicate that a substantial reduction in numbers is possible when vole populations have low intrinsic growth rates, or under higher intrinsic growth rates if barn owl densities are moderate to high. At high vole population growth rates, barn owls can reduce the population to approximately 35% to 85% of the environmental carrying capacity, and at very high barn owl densities of 2 pairs per hectare, can even drive voles to extinction. However, the complex natural fluctuations that occur in *Microtine* populations are not captured in our models, and studies that have studied these processes have had hypotheses or findings that predators are unlikely to play a significant role in limiting population growth of rapidly increasing or peak populations. For example, very few field studies have demonstrated that raptors have been a significant contributing factor in the decline of *Microtine* populations (but see, Maher 1970).

The lack of data on the population dynamics of pocket gophers and voles from agricultural fields made constructing models challenging. The majority of the data published on these key pest species is from rangelands, orchards, alfalfa, and natural grasslands, and shows that populations can significantly vary in reproductive rates, mortality, and territory sizes under different environmental and habitat conditions. Additionally, most of the data we were able to extract for barn owl diets came from vineyards, yet barn owl diet varies significantly with different crop types (Kross et al. 2016), suggesting that the owl and gopher data we used for our models may not overlap. Our models still provide important baseline information, a framework for reassessment when additional data are collected on these species in the same habitats, and an indication that future studies should focus on quantifying the effect of establishing barn owl predation on gopher and vole population densities, reproduction, and survival rates.

Furthermore, while studies to describe the relative importance of different prey species in the diets of owls are common, there has only been one study of a single barn owl nest to quantify the feeding rates and behavior of owls (Browning et al. 2016), which we used as a key

component to estimate prey capture rates of owls. Most studies of barn owl diets utilize pellet analysis, which is a method that produces accurate estimates of prey selection in raptors, but which relies on estimating the minimum number of individuals (Marti et al. 2007), an imperfect method for measuring the number of prey items consumed. Direct methods, such as visual observations through video, are more accurate for understanding prey consumption rates (Lewis et al. 2004). Parameters such as attack rate, search time, and handling time are also important to understanding the true impact barn owls can have on rodent populations. We stress that a field experiment to simultaneously collect data on barn owls and rodent pest populations in an agricultural setting is essential for creating accurate models. The models we have created for this project are flexible and can be easily re-run with new data from field experiments, and therefore provides a framework that can be utilized in the future for shaping an IPM program for rodent control using barn owls.

Avian predators are able to respond to growing prey populations by moving into an area quickly and producing more offspring in years of high prey abundance (Korpimaki 1985, Therrien et al. 2014), so owls in our study area may increase in numbers through both migration and increased breeding success under dense rodent population conditions. Our models assumed that barn owl predation pressure remained similar as prey populations changed. However, optimal foraging theory predicts that owls may spend substantially less time hunting in a particular area, especially as a prey base shrinks or to avoid creating hyper-vigilant populations of prey in a single area (Brown et al. 1999). This needs to be considered as the actual utility of owls could be substantially reduced if their time spent hunting on a particular property is also reduced; the utilization of barn owls as a control method may need to be designed at the scale of the landscape, not just within a single field or farm.

Predators can affect prey populations through both direct predation and indirect changes, such as causing alterations in prey behavior (Lima and Dill 1990, Peckarsky et al. 2008). Our models take into account only direct effects of predators, and do not account for potential behavioral changes in rodent populations as a result of increased predator abundance. Establishing barn owl populations using nest boxes has the potential to substantially increase the population of predators, which is likely to cause changes in the

foraging and breeding behavior of rodent pests (Koskela et al. 1996, Wolff et al. 1999). Only field experiments that monitor these variables will inform whether our models need to incorporate changes in prey breeding output under different owl densities.

Because of our reliance upon only a few single-species studies on the breeding and survival data of pocket gophers and voles, we ran separate, single-prey species Lotka-Volterra models for this study. However, both pocket gophers and voles are commonly found in the same agricultural fields, and barn owls hunt for both prey types simultaneously (gopher and vole remains are often found in the same pellet in diet studies, SMK pers. obs.). Pocket gophers and voles also compete for food and space resources, and high numbers of one species can lead to lower numbers of the other (Klaas et al. 1998). The same attack rate was used in our models for pocket gophers and for voles, however voles may be more vulnerable to attack by barn owls than pocket gophers because of behavioral differences. We recommend that future research should also include further exploration of the use of a Type-III functional response, reflecting that barn owls will switch to a different prey when primary prey are reduced in density. The Type-III response is s-shaped and includes learning time and prey switching based on the abundance of prey. However, this functional response requires more refined parameters, and therefore cannot be tested until more empirical data is obtained. This functional response may alter the predicted long-term persistence of rodent populations thereby provide a more realistic simulation of prey capture behavior.

We built our models using seasonal timesteps to provide results that are on a realistic management timescale for farmers, but we used an annual average for owl hunting effort and rodent reproductive output, rather than including variation in these variables across seasons. Barn owls in agricultural habitats in the Western United States consume mostly juvenile pocket gophers (Van Vuren et al. 1998, Browning et al. 2016, Kross and Baldwin 2016, Kross et al. 2016) during the breeding season, but most likely consume adults and sub-adults in late summer through early winter when juvenile availability is lower. Better understanding of how barn owl prey preferences and predation risk for rodents change seasonally will build more detailed and relevant predator-prey models.

Our models are necessarily simplistic given data limitations. As such, counter to our model outcomes, barn owls are not likely to lead to a population-level extinction event for rodents in a particular area since owls are likely to switch to a more abundant food source or emigrate when prey populations are low. Our models do suggest that barn owls are likely to lead to some equilibrium level in prey populations. Whether or not this level is sufficiently low will depend on grower preference. Determining what an acceptable population of rodent pests is in a field is an important component of IPM, where thresholds are used for determining further pest management actions. If numbers rise substantially above this threshold, further removal efforts may be needed, such as trapping, burrow fumigation, or rodenticides. Importantly, field data is unavailable to understand whether further reducing target rodent populations through additional removal efforts will result in reduced owl hunting capacity, with potential effects on owl breeding performance, emigration from the area, and possibly lower pest control services from the owls. From a management perspective, even in situations where barn owls can reduce rodent populations to a desirable lower equilibrium, the timescale upon which owls are able to colonize a new area and achieve these results may not be acceptable to growers. Our models suggest that barn owls are able to reduce populations over a faster timeframe if rodents are already at reduced densities, so partnering the establishment of barn owls with efforts to reduce or maintain low rodent populations should be considered. However, field studies to understand the minimum prey base upon which barn owls rely are essential. Such studies should include non-pest species when possible to determine their potential utility at maintaining barn owl populations in areas where rodent pest populations have been reduced to a desired level.

Conclusion

This study provides enough evidence to support some utility of barn owls for managing rodent pests, but additional field trials are needed to understand the biological complexities that we were unable to include in our models. If proven effective, barn owls would provide a very useful tool for managing rodent pests with minimal impacts on the natural environment, and reduced labor and costs compared with other rodent management methods. However, even if

highly effective, our models indicate that natural predation will not manage rodent populations at an acceptable level at all times and in all situations, for example when rodent population growth rates are very high or if owl populations are at very low densities. An IPM Program incorporating barn owls for rodent control is therefore likely to require additional tools.

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