DISSERTATION

BREEDING SUCCESS, PREY USE, AND MARK-RESIGHT ESTIMATION OF BURROWING OWLS NESTING ON BLACK-TAILED PRAIRIE DOG TOWNS: PLAGUE AFFECTS A NON-SUSCEPTIBLE RAPTOR

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY REESA CATHELINE YALE CONREY ENTITLED BREEDING SUCCESS, PREY USE, AND MARK-RESIGHT ESTIMATION OF BURROWING OWLS NESTING ON BLACK-TAILED PRAIRIE DOG TOWNS: PLAGUE AFFECTS A NON-SUSCEPTIBLE RAPTOR BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

BREEDING SUCCESS, PREY USE, AND MARK-RESIGHT ESTIMATION OF BURROWING OWLS NESTING ON BLACK-TAILED PRAIRIE DOG TOWNS: PLAGUE AFFECTS A NON-SUSCEPTIBLE RAPTOR

Introduced pathogens such as the bacterium (*Yersinia pestis*) that causes plague can have far-reaching effects on native ecosystems that go beyond the mortality of infected individuals. We investigated the effects of plague, prairie dog town dynamics, and rainfall on burrowing owls (*Athene cunicularia*) nesting in black-tailed prairie dog (*Cynomys ludovicianus*) burrows in the shortgrass steppe of northern Colorado. We examined effects on prey use, nest density, and breeding success, and used mark-resight methods for owl population estimation. Prairie dogs experience high mortality from plague, and their colonies are periodically extirpated by outbreaks. Plague does not make owls sick, but they may be affected as unmaintained burrows collapse, vegetation grows taller, and the anti-predator benefits of prairie dog association are lost.

From 2005 – 2008, we monitored 322 nest attempts by 311 burrowing owl pairs on the Pawnee National Grassland and collected regurgitated pellets and prey remains. We banded owlets in 2007, and our first objective was to use a mark-resight protocol to estimate abundance, apparent survival, and temporary emigration. The Poisson-log normal mark-resight model (McClintock and White 2009) has recently been implemented in Program MARK (White and Burnham 1999). This model improves upon previous mark-resight models because individual identifications are not required 100% of the time, and individuals may die or be temporarily unobservable. Modeling showed that owlets in better condition that weighed more at first capture had higher survival throughout the summer and were more likely to be above ground. Our suggested improvements to field protocols should improve abundance estimation in the future.

Our second objective was to examine the effects of precipitation, nest density, and plague on prey use and to determine whether prey composition influenced nest or fledging success. We quantified prey use and then analyzed diet composition using multi-response permutation procedures (MRPP) and indicator species analysis. Burrowing owls ate a huge variety of prey dominated by beetles, grasshoppers, ants, rodents, and songbirds. Insects comprised 95% of their diet by number, but only 11% by biomass. Owls in the driest year of our study and those at successful and very productive nests ate fewer birds and more mammals. Owl diet was unchanged by plague outbreaks, except that several bird species were less commonly eaten following epizootics. It appears that burrowing owls often forage outside of prairie dog towns, making town-level differences less relevant to owl diets.

Our third objective was to determine the effects of plague, prairie dog town dynamics, and rainfall on nest fate, fledging success, and distances from each nest to its three nearest neighbors. Generalized linear modeling showed that rainfall was the strongest predictor of nest and fledging success, with higher rainfall associated with lower breeding success. Nests were more likely to succeed when plague events were more recent, and they produced more fledglings on towns where any extirpation was brief, and prairie dogs were otherwise resident on site for a longer time. Nests were closest together on recently plagued towns where prairie dog activity had been nearly continuous for a long time and recolonization was rapid. Although ubiquitous on active prairie dog towns, burrowing owls were nearly absent from towns that were not recolonized after plague epizootics.

Both precipitation and plague influenced population dynamics of breeding burrowing owls. We found strong relationships among rainfall, prey species composition, and owl breeding success, and only half the owlets that emerged from burrows survived to fledge during the wettest July of our study. Precipitation regimes are expected to become more extreme in the future, which will likely have consequences for burrowing owls and other dryland species and may affect the size and frequency of plague outbreaks (Stapp et al. 2004). Although owls were absent from towns that were not recolonized after plague epizootics, it appears that burrowing owls can adapt to plague and even benefit in some cases. If conservation of burrowing owls is a primary goal, our results suggest that it will be more useful to preserve prairie dog habitat and connectivity between towns at a landscape scale than to intensively manage plague.

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CHAPTER 1

OVERVIEW OF DISSERTATION

Wildlife diseases are increasingly recognized as important to conservation and population dynamics (e.g., Pedersen et al. 2007; Hudson et al. 2001). For example, chytrid fungus in amphibians (Daszak et al. 1999), parvovirus and canine distemper in African carnivores (Roelke-Parker et al. 1996), and chronic wasting disease in deer and elk (Williams and Miller 2002) have large consequences for affected species, with many scientific and popular news articles published on these topics. Some of the most severe responses to disease occur as a result of non-native species introductions. Parasite (macroparasite or microbial pathogen) spillover occurs when a novel parasite is introduced to a native host, while parasite spillback occurs when a native parasite is amplified by an abundant introduced host and then spills back in greater numbers to a native host (Kelly et al. 2009).

Disease may also have large indirect effects on non-susceptible species, but these get far less attention (Antolin et al. 2002). However, several diseases of keystone species and ecosystem engineers, in which either the pathogen or an abundant new host is non-native, are known to cascade through communities or ecosystems. For example, the Black Death (plague) caused by the introduced bacterium *Yersinia pestis* killed huge numbers of medieval humans, resulting in agricultural decline in Europe and large-scale forest regrowth (van Hoof et al. 2006). Southern sea otter (*Enhydra lutris nereis*) populations are constrained by numerous toxins, macroparasites, and pathogens, including *Toxoplasma gondii* and *Sarcocystis neurona* contracted from the feces of introduced domestic cats and opossums, respectively (Jessup et al. 2007; Johnson et al. 2009; Miller et al. 2010). Sea otter declines have cascading effects that lead to decline of the kelp forest and associated community (Paine 1969; Estes and Duggins 1995; Power et al. 1996). Modern plague-caused mortality of black-tailed prairie dogs (*Cynomys ludovicianus*) has recently been implicated in declines of mountain plover (*Charadrius montanus*) nesting (Augustine et al. 2008) and occupancy of extirpated prairie dog towns (Dinsmore and Smith 2010).

Plague was first introduced to western North America in 1899 (Dicke 1926; Link 1955; Antolin et al. 2002) and to northern Colorado around 1948 (Ecke and Johnson 1952). Disease has been reported from at least 76 species of mammals in the western U.S., with high mortality in black-tailed prairie dogs (Barnes 1993; Cully and Williams 2001). Epidemics typically wipe out entire colonies, so instead of living in extensive towns as they once did, prairie dogs exist in metapopulations of smaller towns that periodically go extinct and are recolonized (Antolin et al. 2002; Stapp et al. 2004). Because black-tailed prairie dogs are considered ecosystem engineers and keystone species (Miller et al. 1994; Kotliar et al. 1999; Kotliar 2000; Miller et al. 2000; but see Stapp 1998), local extirpation of towns might be expected to affect many town associates (Antolin et al. 2002; Lomolino and Smith 2004; Smith and Lomolino 2004; Stapp et al. 2008) in addition to mountain plovers and black-footed ferrets (*Mustela nigripes*: Williams et al. 1994; Matchett et al. 2010).

We studied the effects of introduced plague on a non-susceptible avian associate of prairie dog towns, the burrowing owl (*Athene cunicularia*). Burrowing owls are small ground-dwelling raptors of the prairies that can be active at any time of day, hunting a wide variety of insects, mammals (but not prairie dogs), birds, and other prey (Conrey Ch. 2). In the northern United States and Canada, most populations are migratory, nesting in burrows dug by mammals such as prairie dogs and ground squirrels (Haug et al. 1993). Black-tailed prairie dog burrows in Colorado are used for nesting and refuge, and mounds are frequently used as perches. Plague does not make owls sick, but they may be affected as unmaintained burrows collapse, vegetation grows taller, and the anti-predator benefits of prairie dog association are lost. These may include increased visibility from trimming of vegetation, alarm calling, and providing an abundant alternate prey source (Hoogland 1995). Burrowing owls are widely distributed on the prairies of North, Central, and South America, but they are a declining and protected species in many areas and are a state-listed threatened species in Colorado (Colorado Division of Wildlife 2007).

To our knowledge, no one has studied the effects of plague on burrowing owls, despite the importance of plague in structuring habitat and determining whether or not an area is usable for nesting. Several studies have found that owls prefer active to inactive prairie dog towns (e.g., Butts and Lewis 1982; Toombs 1997; Orth and Kennedy 2001; Sidle et al. 2001; Tipton et al. 2008), but the effects of prairie dog extirpation and time to recolonization were unknown. Count data from the U.S. Forest Service on the Pawnee National Grassland (PNG) of northern Colorado suggested that owl numbers were generally tracking the increasing area occupied by prairie dogs (Conrey, unpub. data).

Similarly, Desmond et al. (2000) found that owl numbers tracked prairie dog populations in the Nebraska panhandle with a time lag in the response of owl numbers to prairie dog population declines. Burrows in Oklahoma filled within 3 years of prairie dog removal via cultivation and poisoning (Butts and Lewis 1982). However, Hoogland (1995) noted that burrowing owls seemed common in prairie dog towns that had recently declined due to poisoning or plague, which mirrored our own initial observations on the PNG.

We studied the effects of plague on breeding owls, as measured by nest fate (success or failure), fledging success (fledglings per nest), and distance between nests. The effects of precipitation were also of interest, because rainfall was quite variable during our study, it is the most important environmental factor governing ecology on the shortgrass steppe (Lauenroth and Sala 1992), and it influences the likelihood of plague epizootics (Stapp et al. 2004). In addition, high precipitation may lead to reduced breeding success in burrowing owls and other raptors (Village 1986; Steenhof et al. 1997; Wellicome 2000; Ronan 2002; Griebel and Savidge 2003) due to decreased foraging efficiency.

Our assessment of breeding success required an accurate count of owlets, but we knew counts would be biased low (Gorman et al. 2003) because owlets may be underground or otherwise undetectable during observations. We used the Poisson-log normal mark-resight (M-R) model (McClintock et al. 2009; McClintock and White 2009) to estimate abundance (Conrey Ch. 2) in 2007, with the goal of quantifying the amount of bias in visual counts and accounting for it in other towns and years. Our abundance estimates were unfortunately biased low, so we could not assess further bias in visual counts. However, by adopting a robust design that incorporated both closed and open intervals when recruitment, mortality, immigration, and emigration were permitted (Kendall et al. 1995; 1997), we had better success with estimation of apparent survival and temporary emigration (underground) of owlets. Survival over a 4-week period, which is approximately the time from emergence to fledging, averaged 0.500 ± 0.079 in a poor (wet) year for owl reproduction. Owlets with better body condition at first capture had higher survival throughout the summer, and those weighing more at first capture had a higher probability of remaining above ground. This is one of the first applications of a new robust M-R model that is unique in allowing individuals to die or leave the study area, permitting < 100% individual identification of marked animals, and providing efficient parameter estimation in a likelihood-based framework (McClintock and White 2009).

From 2005 – 2008, only two nests of 322 that we monitored were off prairie dog towns, and just one nest was located on a town that had been inactive (without prairie dogs) for > 2 years. Owls nested on all towns that had experienced plague epizootics since 2004 and then been recolonized, but they nested mainly on the small portions of these towns with prairie dog activity. Our next question related to the mechanism responsible for these patterns in owl nesting behavior. First, vegetation is shorter with lower biomass on towns than off towns or on extirpated towns, with different species composition and more bare ground (Hardwicke 2006; Hartley 2006; Hartley et al. 2009), but these changes are patchy in space and time and depend on topography (e.g., location on hills or swales) and rainfall. Second, although burrows eventually collapse and become unusable for owl nesting, more are available in the shorter term after prairie dog numbers have been reduced. Burrowing owls require more than just the nest burrow;

mounds are used for perching, and multiple satellite burrows are used by adults and juveniles for rest and refuge. Third, after epizootics, fewer prairie dogs (or none) are available to alarm call or feed predators like snakes, badgers, and larger raptors. Finally, the changes in vegetation and digging activity that accompany prairie dog extirpation may lead to changes in the prey community and in owl diets. Rodent (Stapp 2007; Stapp et al. 2008) and arthropod (Bangert and Slobodchikoff 2006) communities are known to differ on active and inactive towns.

We investigated this last potential mechanism for plague effects on owls. We quantified owl diet and examined ecological factors related to prey use, including year, rainfall, plague, nest density, and breeding success (Conrey Ch. 3). Burrowing owls in our sample ate at least one of almost every available prey item on the PNG, including almost every small rodent known to occur there, as well as insects dominated by beetles and grasshoppers, birds, arachnids, reptiles, amphibians, and crayfish. There was a large difference in prey counts dominated by insects (95%) and prey biomass dominated by rodents (67%). Grasshoppers were more commonly eaten in a dry year, and some but not all vertebrate species were consumed less often at nests on towns with higher nest density. Owls in the driest year of our study and those at successful and very productive nests ate fewer birds and more mammals. Diet was mostly unchanged by plague. Our diet composition data suggest this is because owls often forage for vertebrates off towns, making more localized changes on towns less important.

Finally, we studied the effects of plague and variation in rainfall on breeding burrowing owls, including nest fate, fledgling counts, and average distance to the three nearest nests (Conrey Ch. 4). Our study occurred in years with varying rainfall and on towns with varying histories of plague and prairie dog occupation. Rainfall was the best predictor of breeding success, and higher summer rainfall was associated with nest failure and fewer fledglings per nest. More recent plague was associated with nest success and more closely spaced nests. Older towns where prairie dogs had been absent for no more than 2 consecutive years since data collection began in 1981 had more fledglings per nest and closely spaced nests. Apparent nest success averaged 62% in wet years and 84% in dry years. Fledging success across all owl pairs averaged 2 owlets in wet years and 3.4 owlets in dry years. Successful pairs averaged 3 – 4.5 fledglings (range 1 – 9). Mean distance to the nearest nest was 249.6 ± 588.9 m on prairie dog towns and 188.3 ± 164.7 m on towns with more than one nest.

Our results have implications for conservation and wildlife management where climate change and disease effects are a concern. We found strong relationships among rainfall, prey species composition, and owl breeding success. In addition, only half the owlets that emerged from nests survived to fledge during the wettest July of our study, in which one storm contributed 1/5 the total mean annual precipitation. Precipitation regimes are expected to become more extreme (Easterling et al. 2000; Karl and Trenberth 2003; Goswami et al. 2006; Allan and Soden 2008; Groisman and Knight 2008; Knapp et al. 2008; Heisler-White 2009), with larger storms separated by longer dry periods. On the shortgrass steppe, above ground net primary productivity (ANPP) should increase as a result (Heisler-White 2009), but our results suggest that not all dryland species will benefit. Burrowing owls and other dryland species may respond in unexpected ways, and altered precipitation regimes may influence the likelihood of plague outbreaks (Stapp et al. 2004).

Burrowing owls in our study benefited when plagued towns were quickly recolonized by prairie dogs, but were absent otherwise. This suggests that intensive management of plague via vaccination programs or flea control is generally not needed if burrowing owl conservation is the primary goal and connectivity between prairie dog towns is adequate. Plague management may be important for isolated towns (Cully et al. 2010) that are unlikely to be quickly recolonized or wherever conservation of other species like black-footed ferrets is a priority (Williams et al. 1994; U.S. Fish and Wildlife Service 2009; Biggins et al. 2010; Matchett et al. 2010). Towns in historically plague-affected regions are smaller, farther apart, and occupy less of the available area than towns in regions with no plague (Cully et al. 2010). However, connectivity on the PNG is high, as evidenced by the rapid recolonization of towns we observed and by the 39% misassignment rate observed by Roach et al. (2001); individuals that did not genetically assign to the town where they were captured were likely migrants or descendants of migrant prairie dogs.

We recommend that managers focus on conservation of habitat for prairie dogs and maintenance of connectivity among towns. The positive effects of connectivity (recolonization of extirpated towns) should generally outweigh negative effects of increased disease transfer (Cunningham 1996) or social responses of prairie dogs to increased numbers of migrants, such as aggression, infanticide, stress, or vigilance (Hoogland 1995). Isolation may not reduce vulnerability to plague (Stapp et al. 2004). However, these issues should be considered when forming management plans. Antolin et al. (2002) suggested conserving complexes of towns where all towns are within 7 km of another town to account for movement capabilities of prairie dogs and ferrets. Subject to future changes in precipitation regimes, burrowing owls have the potential to persist and even increase in the presence of introduced plague as long as prairie dogs are conserved at a metapopulation scale.

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CHAPTER 2

MARK-RESIGHT ESTIMATION OF APPARENT SURVIVAL, TEMPORARY EMIGRATION, AND ABUNDANCE FOR JUVENILE BURROWING OWLS

ABSTRACT

Quantifying the number and survival rate of juveniles is a common goal for researchers and wildlife managers, but many populations present challenges to unbiased estimation. For example, visual counts may result in underestimates for species with mobile young. The Poisson-log normal mark-resight model (McClintock and White 2009) is useful for situations when i.) individuals can be marked and then observed without recapture, ii.) marked and unmarked individuals are equally visible, iii.) sampling with replacement may occur, iv.) marks are individually identifiable but identification is < 100%, and v.) the number of marks may be unknown (individuals may die or leave). Abundance, apparent survival, and temporary emigration are estimated. Parameters may be shared among groups of individuals, and individual and environmental covariates can be included in models implemented in Program MARK (White and Burnham 1999). We applied this method to burrowing owl (*Athene cunicularia*) juveniles on the Pawnee National Grassland, Colorado in 2007. Owlets in better condition that weighed more at first capture had higher survival throughout the summer and were more likely to be above ground. Although estimates of abundance were biased low, our recommended changes to field protocols should improve estimation in the future.

INTRODUCTION

Estimation of reproductive rates often requires the counting of juveniles and assessment of their survival until fledging. However, juveniles can be difficult to observe and count accurately, particularly for those species that nest or roost in relatively inaccessible areas. Burrowing owls (*Athene cunicularia*) have a rather unique life history among owls because they are diurnal and ground-dwelling. Burrowing owl juveniles are relatively easy to observe on the shortgrass steppe when above ground, but owl nests are underground and often located in black-tailed prairie dog (*Cynomys ludovicianus*) burrows in Colorado (VerCauteren et al. 2001). Following first emergence from the nest burrow at 12 – 14 days (d), owlets continue to spend time underground and retreat into burrow entrances to rest or when threatened. This means that owlets are sometimes undetectable underground. In addition, they run and eventually fly outside of the nest for more than a month before becoming independent of their parents.

Previously, visual counts were used as a minimum abundance estimate at each nest, but these estimates are known to be biased low (systematic underestimation of unknown magnitude) with unknown probability of detecting owlets (Gorman et al. 2003). Knowing that owlets may sometimes be underground and undetectable, our goal was to more accurately count owlets, assess their survival to fledging age, and determine what factors influence these estimates. Capture-mark-recapture methods (Otis et al. 1978; Kendall et al. 1995; 1997) are widely used to obtain unbiased estimates of abundance and survival by accounting for imperfect detection probabilities. These methods may be modified for less handling by resighting rather than recapturing individuals after they have been marked with field-readable bands (Spendelow et al. 2002). However, the number of marked animals in the population and the number of resightings per marked individual must be sufficiently large for this approach to be useful. Because fewer than 20 marked juveniles were expected from each prairie dog colony in our sample and perfect individual identification was unlikely, a different approach was needed. Mark-resight methods (White and Shenk 2001; McClintock et al. 2006) incorporate data from unmarked individual sightings and require fewer marked individuals than previous approaches (e.g., Spendelow et al. 2002), but the number of marked individuals present in the population must be known. Most existing mark-resight models (e.g., Bowden and Kufeld 1995) cannot account for an unknown number of marks, which might result from mortality or emigration. Arnason et al. (1991) developed a mark-resight model for unknown numbers of marked individuals, but McClintock et al. (2009) described a number of key limitations to this model, including the necessity of 100% individual identifications and the inability to combine data across sampling periods.

The Poisson-log normal mark-resight (hereafter, M-R) model (McClintock and White 2009; McClintock et al. 2009) was developed for situations when i.) individuals can be marked and then observed without recapture, ii.) marked and unmarked individuals are equally visible, iii.) sampling with replacement may occur (individuals may be counted multiple times during secondary occasions/scans), iv.) marks are individually identifiable but individual identification is < 100%, and v.) the number of marks may be unknown (this can be estimated). In our study, each observation consisted of multiple scans of the nest area and counts of observable owlets. With the exception of the morning after banding, the number of marked burrowing owls is unknown because owlets may fledge and leave the nest area or die between observations. Other assumptions are the same as for Bowden's estimator (Bowden and Kufeld 1995): closure (no birth, death, immigration, emigration, or loss of marks) between scans within observations, no errors in distinguishing marked from unmarked individuals, and the same resighting probabilities (independently and identically distributed) for marked and unmarked individuals.

We used a robust design (Kendall et al. 1995; 1997): scans were repeated multiple times per observation and observations were repeated from the time owlets emerged from burrows until they fledged. In a robust design, the population must be closed during the multiple scans (secondary occasions) that make up each observation (primary occasion). The population can be open between primary occasions. Abundance can be estimated for each observation, which in our case consisted of 8 – 10 scans. Parameters related to mean resighting rate for owlets and individual heterogeneity arising from individual differences in sightability that cannot be explained by weight, age, or any other measured variable are also estimated (McClintock and White 2009; McClintock et al. 2009). The advantage of a robust design is that apparent survival (probability of surviving and remaining in the survey area) and temporary emigration can be estimated during open intervals, whereas previous M-R models emphasized estimation of abundance only (McClintock and White 2009).

Estimates of abundance from the M-R model apply to groups of nests rather than to individual nests. Individual nests do not include enough owlets to provide adequate sample size, and some nests on the study site may not have any marked owlets but can still be included in the analysis. Estimates apply to owlets old enough to be sighted above ground. This approach has the potential for wide application in population demographic studies of any species where marking and individual resighting is feasible.

Additional motivations were conservation concerns and interest in how owl reproduction is affected by plague, which is caused by the introduced bacterium *Yersinia pestis* and decimates black-tailed prairie dog towns. In the northern United States and Canada, most owl populations are migratory, nesting in burrows dug by mammals such as prairie dogs and ground squirrels (Haug et al. 1993). Prairie dog burrows on our site are used by owls for nesting, satellite burrows are used for rest or refuge, and mounds are used as perches. Plague does not make owls sick, but unmaintained burrows collapse, vegetation grows taller, and the anti-predator benefits of prairie dog association are lost. Burrowing owls are widely distributed on the prairies of North, Central, and South America, but they are a declining and protected species in many areas and are a state-listed threatened species in Colorado (Colorado Division of Wildlife 2007). This small owl may be active at any time of day or night and hunts a wide variety of vertebrates and invertebrates (Conrey Ch. 3).

We had four objectives.

1. Illustrate the use of the new Poisson log-normal M-R model for estimating abundance, apparent survival, and temporary emigration.
2. Compare estimates of abundance from the M-R model to those from visual counts.
3. Determine the effects of weight and body condition at first capture on apparent survival of burrowing owls and the probability of being underground and unavailable for resighting. We hypothesized that larger owlets in better condition would have higher survival and be more likely to remain above ground.

4. Measure the relationship of apparent survival with owlet age. We hypothesized that apparent survival would increase with owlet age until fledging and then decline as owlets began to leave the nest vicinity.

Our first hypothesis (objective 3) was based on the assumption that larger juvenile raptors were typically born earlier than their siblings and have a competitive advantage (Mock 1984; Gill 2007). They may be healthier and more active than smaller juveniles. Therefore, we hypothesized that larger owlets in better condition would have higher survival and be able to remain more active above ground than smaller, thinner birds. Following first emergence from the nest, we often observed owlets swarming from the nest to surround adults with food. An alternative hypothesis was that smaller owlets are forced to risk predation by remaining above ground more often in order to be the first to greet adults returning with food.

Our second hypothesis (objective 4) was based on our observation that nests with older owlets tended not to fail, particularly after owlets could fly and appeared to be more vigilant toward humans and predators. Younger owlets sometimes would not flee from us unless their parents were nearby and vocalized to them, and we occasionally caught them by hand during trapping. We thought that true survival would improve with owlet age while parental care continued, but apparent survival would eventually decline as owlets fledged and left the nest area.

METHODS

Study Site

Our study site (Fig. 2.1) on the Pawnee National Grassland (PNG) is located in the shortgrass steppe (SGS) of north central Colorado (Weld County). The SGS covers the central and southern Great Plains, the driest and warmest part of America's central grasslands (Lauenroth and Burke 1995; Pielke and Doesken 2008). The area managed by the USDA Forest Service PNG consists of 78,128 ha spread over a larger 50 x 100 km region with a patchwork of public and private ownership. We worked mainly in the northwestern PNG, which has mean elevation of 1650 m and mean annual precipitation of 321 mm, with > 70% of this falling as rain from April – September (National Climatic Data Center 2002; Pielke and Doesken 2008). The amount, timing, and intensity of precipitation are the most important factors in determining the ecology of the SGS (Lauenroth and Sala 1992). Most precipitation events on the PNG are small, with much of the water lost to evapotranspiration (Sala et al. 1992; Lauenroth and Bradford 2006). More than 80% of the PNG is upland steppe habitat (Hazlett 1998). The two dominant species are perennial C_4 warm-season grasses: blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*). Other common species are prickly-pear cactus (*Opuntia polyacantha*) and two dwarf shrubs: rabbitbrush (*Chrysothamnus nauseosa*) and saltbush (*Atriplex canescens*) (Lauenroth 2008).

Livestock grazing (mostly cattle) is the dominant land use across the PNG, and cattle were common on our study areas. Bird-watching and recreational shooting are also common on the PNG. Recreational shooting of legal and illegal targets occurred throughout the study period, and an 8.5 month open season (mid-June through February annually) on prairie dogs was reinstituted in June 2007 after a six year moratorium. Extensive shooting occurred on several easily accessible towns, especially towns 51 and 78, with moderate shooting on all towns near gravel roads open to the public, and very little shooting on more isolated towns.

In a state-wide survey of Colorado, 80% of burrowing owl locations were on prairie dog colonies, and 24% of locations were in Weld County (VerCauteren et al. 2001). Burrowing owl occupancy in Colorado was highest on active prairie dog towns, followed by inactive towns, and all towns had much higher occupancy than grassland or dryland agriculture (Tipton et al. 2008). During three surveys of nine randomly-selected quarter sections (64.75 ha), we found only one nest that was not on a prairie dog town; another two off-town nests were discovered by chance. This compares to 320 nests located on prairie dog towns, which have been mapped by the Forest Service since 1981. The area occupied by these towns has increased since 1981 with an exponential increase since the mid-1990s. Declines in area occupied have occurred during recent plague epizootics, but due to rapid recolonization and the colonization of new towns, the total area occupied has remained around 1 – 2% of the PNG.

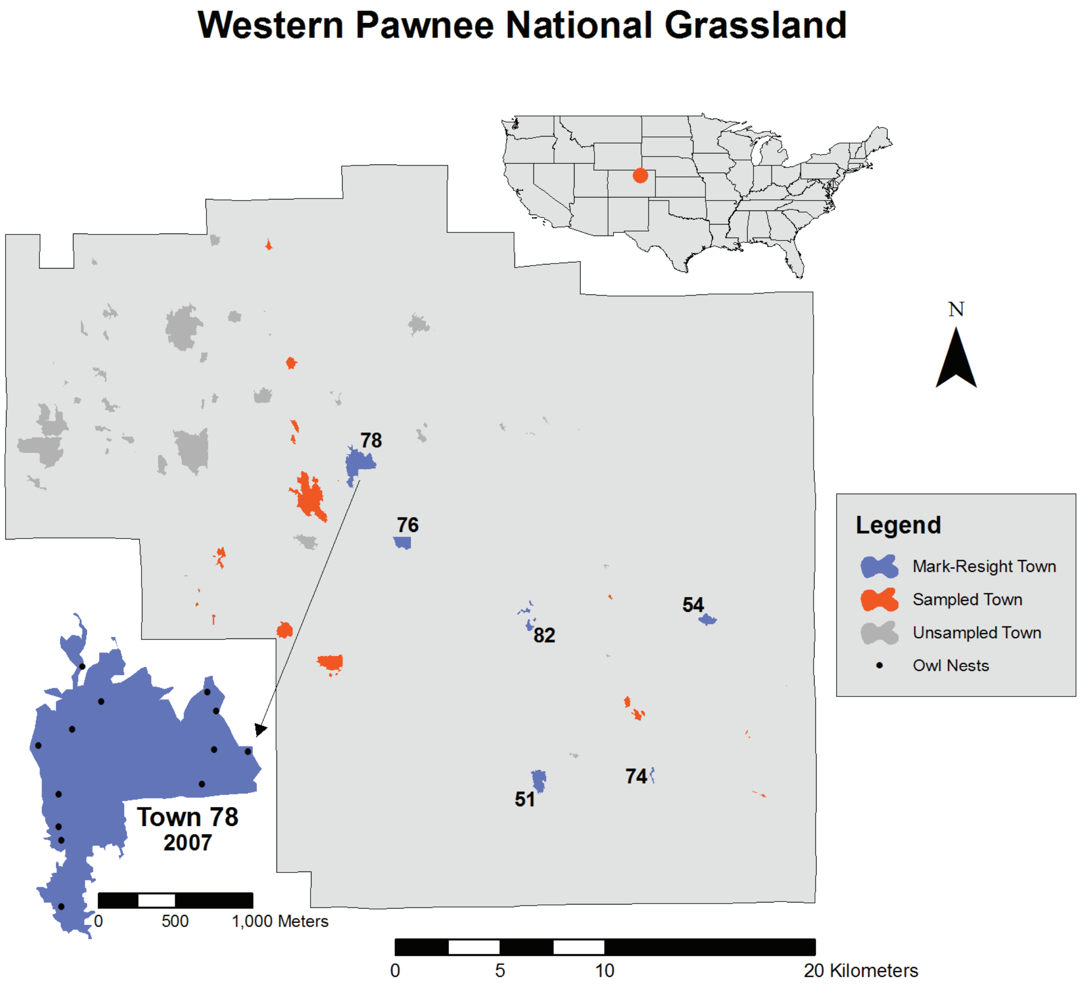

Figure 2.1. Prairie dog towns are displayed at their maximum extent for 2006 – 2007. In either year, the total area occupied by prairie dog towns was slightly less than the displayed area because of colonizations, extinctions, and other fluctuations in town size. Mark-resight occurred on the six labeled towns during 2007, but 2006 town area is included because owls in 2007 occasionally nested on unmapped portions of extirpated towns with little or no prairie dog activity. Visual counts occurred on all sampled towns.

Nest Searches

We searched for adult owls on prairie dog towns and then looked for nest burrows in the vicinity of owl sightings. Early in the nesting season, adult males, who are not involved in incubation or brooding, typically perch conspicuously near the nest burrow during the day. Nest burrows were identified by the presence of shredded mammal manure (Levey et al. 2004), owl feathers, regurgitated pellets, and prey remains such as grasshopper legs, rodent tails, and passerine feathers. A burrow was identified as the site of a nest attempt only if shredded manure, typically cow, prairie dog, or canid, was present ("nest lining": Garcia and Conway 2009). We conducted a minimum of three complete surveys on each prairie dog town so that a removal method (Hayne 1949; Otis et al. 1978; White et al. 1982; Rosenberg and Haley 2004) could be used to estimate nest abundance and probability of nest detection.

Trapping and Banding

Juveniles were targeted for banding on six of 25 surveyed towns (Fig. 2.1) following their emergence from nest burrows, which first occurred on June 19, 2007. These six towns were randomly chosen from those with at least five nests (sufficient sample size identified by power analysis) in a stratified sampling procedure based on plague status and town size. Trapping techniques included burrow/tube traps (Botelho and Arrowood 1995), cage/one-way door traps (Banuelos 1997), and noose rods and carpets (Winchell and Turman 1992). Our most successful trap, capable of catching multiple owls at once, was designed by Dr. Brent Bibles. This burrow trap is rectangular, built from a pliable mesh hardware cloth with a one-way door that is inserted into the burrow entrance, with fabric used to block escape around the edges of the door. Trapping in the evening (especially 7 – 11 pm) was much more successful for owlets than morning trapping. Owlets were easier to catch when < 28 d old, and particularly at younger ages before they began spreading into satellite burrows. Trapping was not attempted in steady rain or high temperatures (> 27°C).

All captured owls received a silver U.S. Fish and Wildlife Service numbered band from the Bird Banding Laboratory (now administered by the U.S. Geological Survey). Adults were banded on the other leg with a blue aluminum alpha-numeric coded band (Acraft, Inc.). Juveniles were uniquely color banded with three plastic bands in various combinations of orange, yellow, black, and white. Attempts to read alpha-numeric codes with spotting scopes in 2006 were unsuccessful, so color bands were used in 2007. Owlet ages were determined by plumage characteristics and size (Priest 1997). We also recorded weight, tarsus and wing chord length, parasite load, crop fullness, and body condition (relative amount of fat and muscle over the keel).

Owlets were batch marked with non-toxic paint on the crown and upper breast so that marking status could be determined even when feet (and bands) were unobservable. We used a paint designed for marking livestock (All-weather Paintstik® livestock marker, LA-CO Industries, Inc.). Dr. Bibles first tested black ink on separate study sites in central eastern Colorado, but ink generally did not show up well or last long on feathers. Green, red, and blue paints were easily seen and lasted for over a month. Nearby nests were given different colors of paint, so that owlets could be identified to their nest, even if band codes were not readable. It was important that the paint not obstruct the eyebrow or chin region, because lightening plumage in these areas was used to age owlets. Only owlets were color banded and painted, because adults were not included in the M-R model.

Nest Monitoring

Owlets were counted and aged using spotting scopes during a sequence of 8 – 10 snapshot scans (secondary occasions) for up to 30 min. We did not monitor nests in steady rain, hot (> 27°C), or windy (> 21 km/hr) conditions. Two observers were present at each scan, typically positioned 150 – 250 m from the nest. The primary observer conducted the scans, and the secondary observer helped to identify banded owls and looked for batch marks on those that were difficult to see. For each scan, we categorized owlets as identified (IDd: band code was read), marked but not identified (unIDd), unmarked, or unknown (presence of paint batch mark could not be determined). Owlets of unknown marking status cannot contribute to parameter estimation, so their presence creates estimation bias. They were counted so that degree of bias could be assessed, and strong efforts were made in the field to determine marking status.

Each owlet was aged according to behavior, plumage characteristics, and size (Priest 1997). Maximum information was gained when all owlets were individually aged and when each of these ages was linked with one of the four banding categories (IDd, unIDd, unmarked, or unknown). If ages were not linked to marking status of birds or if owlets could not be aged because our view was blocked or too brief, then owlets were assigned the mean age for that nest. Presence of adults was noted, because lack of adult activity may indicate nest failure, as do prairie dogs in the burrow or cobwebs covering the entrance. Time, temperature, cloud cover, and wind speed were also recorded. These time-varying covariates may influence detectability, and their use in model-building may lead to a more parsimonious model as compared to calculating separate estimates for each primary occasion.

In addition to the scanning protocol required for application of the M-R model, we conducted visual counts to produce an estimate of minimum number known alive (MNA). This protocol does not require that any individuals be marked, so we conducted these visual counts at all nests on all monitored towns in addition to the six towns used for the M-R analysis (Fig. 2.1). We counted owlets for ≥ 15 min. at all nests and recorded the maximum number of owlets at each nest every 5 min., along with their ages. For towns with banded birds, this was done by the secondary observer at the same time that the primary observer conducted the snapshot scans. If we were unsure where an owlet belonged, the secondary observer watched it until it moved to a nest, joined other owlets, or was fed by an adult. In the few cases (fewer than five per year) where the nest could not be identified, the owlet was not counted.

Nests were monitored once per week whenever possible, but the longest interval between observations was 13 days. We monitored each nest until all owlets at that nest were considered to be older than 50 d. Fledging of owlets at each nest may be staggered across a week or more, because females lay one egg every 1 – 2 days and usually begin incubation with the first egg (Bent 1938; Olenick 1990; Haug et al. 1993). Following Haug (1985) and Desmond and Savidge (1999), we used 42 d as fledging age, within the range of 35 – 44 d used by others (Thomsen 1971; Landry 1979; Todd et al. 2003; Davies and Restani 2006; Lantz and Conway 2009). Nests were monitored on the morning following evening banding, when the number of bands in the population was known. On later occasions, the number of bands was estimated in the M-R model.

Analysis

We used the M-R model (McClintock 2008; McClintock and White 2009) to estimate abundance, apparent survival, and temporary emigration throughout the breeding season. We had initially planned a single analysis that would include data from all six towns where the M-R protocol was applied. This would allow some parameters to be shared across towns, potentially leading to more parsimonious models and more precise estimates, while population size would be estimated separately for each primary occasion on each town. However, data from all but town 78, which had the most nests and marked birds, were too sparse to permit this type of analysis with separate abundance estimates for each individual town. Therefore, we analyzed town 78 separately and then conducted a site-wide analysis with all six prairie dog towns included as a single group and with town identity as an individual covariate. This produced a single abundance estimate for each primary interval. In each input file, the capture and resighting histories for IDd birds were followed by counts of unmarked, unIDd, and known marks (App. 1, Fig. 2.5, 2.6). The number of marks was known only for the time occasion immediately following the first night of banding in each town.

We estimated the following parameters for each closed primary occasion: number of unmarked owlets (U), intercept (log scale) for mean resighting rate (α), and individual heterogeneity (σ), which increases the variance of the derived parameters due to differences in resighting rate among individuals. Derived parameters (functions of the above parameters) estimated for closed periods were the expected number of resightings (λ) and total population size (N). For the open intervals between primary occasions, we estimated apparent survival (ϕ) and two parameters for temporary emigration: the probability of transitioning from observable to unobservable (γ'') and of remaining unobservable (γ'). Prior to fledging, this is the probability that owlets remain underground for the entire primary occasion. U was always estimated separately for each primary occasion. Each model contained six parameters: U, α, σ, ϕ, γ'', and γ'.

For marked owlet s during occasion j, the number of resightings (y_{sj}) is modeled as an independent Poisson log-normal random variable with ln(mean resighting rate) α_j treated as a fixed effect and individual heterogeneity treated as a random effect with mean zero and variance σ^2_j (McClintock et al. 2009). The model takes the form of $E(y_{sj} \mid \sigma_j, Z_{sj}, \alpha_j) = \lambda_{sj} = \exp(\sigma_j Z_{sj} + \alpha_j)$ where $Z_{sj} \sim N(0,1)$ are standard normal random variables that are independently and identically distributed. Z_{sj} represents the latent sightability of individual s during occasion j. The total number of unmarked sightings is also needed for abundance estimation. Additional details are given in McClintock and White (2009) and McClintock et al. (2009), with modifications when the number of marks in the population is unknown. McClintock and White (2009) used a slightly different parameterization than McClintock (2008) or McClintock et al. (2009): θ for α, ψ^{OU} for γ'', and ψ^{UO} for $1 - \gamma'$.

We created an *a priori* model set in which parameters were modeled by time and as linear combinations of environmental and individual covariates (Table 2.1) with a separate "beta" coefficient (slope term) estimated for each factor in the linear model. The "t" models allowed each parameter to be separately estimated for each primary occasion or interval, so one beta coefficient was estimated per time interval for each parameter. We also ran more efficient linear and quadratic time trend models that modeled time effects as linear or curvilinear, because we expected that resighting rate would increase linearly with time due to seasonal effects, and both resighting rate and apparent survival may have leveled off or declined later in the season.

Additional *a priori* models used time-varying environmental covariates or individual covariates to estimate parameters (Table 2.1) using linear models. Time-varying environmental covariates included owlet age, temperature, and wind speed. Individual covariates included the town where an owlet was banded, its weight and body condition at first capture. Resighting rate and apparent survival may have depended on owlet age if older owlets spent more time above ground or if resighting rate and survival eventually declined as owlets fledged and began spending more time away from the nest area. Although we did not do scans in poor weather, resighting rate may have been lower in higher temperatures or wind. Temperature and wind speed were not included in the site-wide models, because different towns were sampled on different dates with different weather conditions and were then combined into primary occasions for analysis (App. 1, Table 2.7). Town was included as a covariate because differences among towns in vegetation height, topography, or resident predators may have affected resighting rate or survival. Owlet weight and body condition were included as individual covariates because they may have influenced resighting probability, apparent survival, and the probability of remaining above ground. We hypothesized that heavier, healthier owlets would be easier to see, more likely to survive, and more often above ground. Finally, in the "dot" models, all estimates of a given parameter were constrained to be equal.

Table 2.1. Modeling of parameters in M-R analyses. Parameters were modeled as additive combinations of several ecological factors. U was estimated separately for each primary occasion. γ'' and γ' were either modeled separately or constrained to be equal (random emigration).

Ecological Factor	Town 78 Analysis	Site-wide Analysis
t	$U\ \alpha\ \sigma\ \phi\ \gamma$	$U\ \alpha\ \phi\ \gamma$
T	α	
T2	$\alpha\ \phi$	
age	α	ϕ
age2	$\alpha\ \phi$	ϕ
temp	α	
wind	α	
town		$\alpha\ \phi$
wt	$\alpha\ \phi$	$\alpha\ \phi\ \gamma$
keel		$\phi\ \gamma$
dot	$\alpha\ \phi\ \gamma$	$\alpha\ \phi\ \gamma$
t1	$\alpha\ \sigma$	σ

Parameters are the number of unmarked owlets (U), intercept for mean resighting rate (α), individual heterogeneity (σ), apparent survival (ϕ), and two parameters for temporary emigration: the probability of transitioning from observable to unobservable (γ'') and of remaining unobservable (γ'). t = time (parameter estimated for each primary occasion), T = time trend (linear change with time), T2 = quadratic time trend, age = average owlet age (time-varying), age2 (squared age for quadratic model), temp = average temperature during scans (time-varying), wind = average wind speed during scans (time-varying), town = prairie dog town (individual covariate), wt = weight at capture (individual covariate), keel = body condition at capture = amount of fat or muscle over keel (poor, fair, good: individual covariate), dot = parameter constrained to be equal across time, t1 = fixed to primary 1 value (when number of marks was known). For the site-wide analysis, the α for the first primary occasion (P1) was allowed to differ from subsequent α, because only town 74 had banded birds during P1, and the number of marks in the population was known.

We assessed goodness of fit (GOF) of models to data by examining residuals and by comparing estimates from the M-R model to minimum estimates from visual counts. Residuals were computed for each marked owlet according to the differences in observed and expected counts throughout the breeding season. Unfortunately, none of the GOF procedures in MARK, such as parametric bootstrapping or median c-hat (overdispersion parameter) estimation, are currently implemented for mark-resight models (Cooch and White 2009). Chi-squared GOF statistics cannot be calculated when many possible capture histories are never observed but have some expectation of occurring so that Σ(observed counts) > Σ(expected counts). Data were too sparse to withhold any for model validation. Therefore, we examined deviance and Pearson residuals for pattern and magnitude for the general model (in which all other *a priori* models are nested) and the top (minimum AIC) model. We also compared abundance estimates to MNA and 4-week apparent survival estimates to the number of fledged owlets (42 d) / the number of emerged owlets (14 d). In addition, estimation of individual heterogeneity directly accounted for one important source of overdispersion (McClintock et al. 2009).

Heterogeneity was originally underestimated because with many counts of either 0 or 10 (the maximum number of scans), it appeared that heterogeneity was low and resighting rate was high (σ^2 and α are negatively correlated). When heterogeneity is underestimated, abundance estimates are also underestimated (McClintock and White 2009; McClintock et al. 2009). For this reason we used the σ estimated for the first primary occasion when the number of marked birds was known, from the unconstrained fully time-varying "t" model as a fixed value for σ in other town 78 models. For the site-wide analysis, we wanted to avoid underestimation of heterogeneity and abundance while still reflecting parameter estimate uncertainty in σ. Because σ_1 could be better estimated than σ from later occasions, we continued to allow estimation of σ_1 but fixed later σ values to the town 78 σ_1 from the "t" model.

Because of the large number of parameters and possible combinations, we initially kept the most general structure ("t" models) on the parameters of primary biological interest (U, ϕ, and γ), while finding the best way to model the other parameters. We used Akaike's Information Criterion (Akaike 1973) adjusted for small sample size (AICc: Burnham and Anderson 2002) to rank the models in the set: 26 models for the town 78 analysis and 21 models for the site-wide analysis. Analyses were run with Program MARK (White and Burnham 1999) version 5.0 by selecting the Mark-Resight, Poisson log-normal model. We calculated model-averaged estimates based on AICc weights. Finally, we compared our abundance estimates from the M-R model to MNA obtained from visual counts.

RESULTS

We banded 60 owlets at 26 nests on six prairie dog towns in 2007 (Fig. 2.1). These nests and the other 26 nests without banded owlets on the same towns were used in application of the M-R model. Mean banding age was 24 d, ranging from 11 – 35 d.

We estimated parameters for town 78 alone (Table 2.2) and for all towns together (Table 2.3). We had six observations at town 78 with five open intervals between them; thus six model-averaged estimates were produced for λ and N, five estimates for ϕ and γ'', and four estimates for γ' (Table 2.2). One fewer estimate of γ' is produced because this is the probability of being underground and unobservable for consecutive observations and birds could not have been marked during observation 1 if they had already gone underground and were not present; γ' is first estimated during the second interval between observations. Following banding of juveniles, we had six observations at towns 51 and 74, five at towns 54 and 82, and four at town 76. Based on when we visited each site, we grouped these observations into nine non-overlapping primary occasions with eight intervals between them (App. 1, Table 2.7).

The expected number of resightings per observation ($\hat{\lambda}$ according to a Poisson model) varied from 3.22 to 9.97 (Tables 2.2 – 2.3). The weekly survival estimate for town 78 from the best model was 0.822 (0.068 SE). Therefore, the probability of an owlet surviving for 4 weeks $(\hat{\phi}_{\text{weekly}})^4$, which is approximately the period of time from emergence to fledging, was 0.456 (0.151 SE, calculated using the delta method) on town 78. The weekly survival estimate from the top model for all towns was 0.841 (0.033 SE), so across sites owlets survived from emergence to fledging with probability 0.500 (0.079 SE). Temporary emigration was best estimated by constraining γ'' to be equal to γ' (App. 1, Tables 2.9, 2.11). The probability of an owlet being underground averaged ~ 0.59, but varied over time (Tables 2.2 – 2.3). Estimates of U, α, and σ (App. 1, Tables 2.8, 2.10) were used to calculate estimates of λ and N.

Table 2.2. Model-Averaged Parameters: Town 78. *N* was estimated separately in each primary occasion.

Model-Averaged Parameter	Estimate	SE	LCI	UCI
Expected # Sightings (λ_1)	4.23	0.45	3.36	5.11
Expected # Sightings (λ_2)	5.42	0.40	4.64	6.21
Expected # Sightings (λ_3)	6.52	0.38	5.78	7.26
Expected # Sightings (λ_4)	9.97	0.42	9.15	10.79
Expected # Sightings (λ_5)	3.63	0.41	2.83	4.43
Expected # Sightings (λ_6)	3.22	0.49	2.25	4.18
Total Population Size (N_1)	31.43	4.60	22.41	40.44
Total Population Size (N_2)	14.49	4.61	5.45	23.53
Total Population Size (N_3)	21.68	4.50	12.85	30.50
Total Population Size (N_4)	17.56	3.05	11.59	23.54
Total Population Size (N_5)	17.23	6.24	4.99	29.46
Total Population Size (N_6)	3.80	2.68	-1.45	9.05
Apparent Survival (ϕ_1)	0.824	0.091	0.579	0.941
Apparent Survival (ϕ_2)	0.818	0.096	0.558	0.941
Apparent Survival (ϕ_3)	0.817	0.084	0.598	0.930
Apparent Survival (ϕ_4)	0.823	0.082	0.606	0.934
Apparent Survival (ϕ_5)	0.780	0.208	0.248	0.974
Emigration (γ''_1)	0.626	0.091	0.439	0.781
Emigration (γ''_2)	0.625	0.091	0.437	0.782
Emigration (γ''_3)	0.626	0.091	0.439	0.782
Emigration (γ''_4)	0.624	0.095	0.429	0.786
Emigration (γ''_5)	0.625	0.092	0.436	0.783
Immigration (γ'_2)	0.590	0.133	0.330	0.808
Immigration (γ'_3)	0.590	0.133	0.328	0.809
Immigration (γ'_4)	0.591	0.132	0.330	0.808
Immigration (γ'_5)	0.591	0.132	0.330	0.809

Model-averaged parameters for town 78 are the expected number of resightings (λ), total population size (N), apparent survival (ϕ), and two parameters for temporary emigration: the probability of transitioning from observable to unobservable (γ'') and of remaining unobservable (γ').

Table 2.3. Model-Averaged Parameters: Site-Wide Analysis. All sampled prairie dog towns were grouped together for this analysis. N was estimated separately in each primary occasion. The first emigration estimate was quite high because only one town was banded prior to primary occasion 1, and no marked owlets were identified in that town during primary occasion 2.

Model-Averaged Parameter	Estimate	SE	LCI	UCI
Expected # Sightings (λ_1)	3.75	1.20	1.40	6.10
Expected # Sightings (λ_2)	7.23	1.73	3.83	10.63
Expected # Sightings (λ_3)	4.97	1.73	1.58	8.35
Expected # Sightings (λ_4)	4.70	1.73	1.32	8.08
Expected # Sightings (λ_5)	5.52	1.73	2.13	8.91
Expected # Sightings (λ_6)	6.79	1.73	3.39	10.18
Expected # Sightings (λ_7)	4.20	1.72	0.82	7.58
Expected # Sightings (λ_8)	4.03	1.72	0.65	7.41
Expected # Sightings (λ_9)	7.07	1.73	3.68	10.47
Total Population Size (N_1)	15.32	3.34	8.76	21.87
Total Population Size (N_2)	20.44	3.03	14.50	26.38
Total Population Size (N_3)	63.97	11.87	40.70	87.23
Total Population Size (N_4)	69.76	11.49	47.24	92.28
Total Population Size (N_5)	26.82	6.08	14.91	38.73
Total Population Size (N_6)	52.94	7.90	37.46	68.42
Total Population Size (N_7)	30.40	9.20	12.37	48.44
Total Population Size (N_8)	46.83	11.50	24.29	69.37
Total Population Size (N_9)	10.74	3.23	4.41	17.07
Apparent Survival (ϕ_1)	0.827	0.055	0.692	0.910
Apparent Survival (ϕ_2)	0.833	0.037	0.747	0.894
Apparent Survival (ϕ_3)	0.834	0.036	0.750	0.893
Apparent Survival (ϕ_4)	0.838	0.033	0.764	0.893
Apparent Survival (ϕ_5)	0.842	0.037	0.757	0.902
Apparent Survival (ϕ_6)	0.845	0.041	0.747	0.910
Apparent Survival (ϕ_7)	0.848	0.046	0.733	0.919
Apparent Survival (ϕ_8)	0.849	0.049	0.727	0.923
Emigration (γ''_1)	1.000	0.004	0.993	1.007
Emigration (γ''_2)	0.775	0.092	0.551	0.906
Emigration (γ''_3)	0.317	0.110	0.146	0.558
Emigration (γ''_4)	0.786	0.093	0.553	0.916
Emigration (γ''_5)	0.569	0.124	0.329	0.780
Emigration (γ''_6)	0.798	0.099	0.543	0.929
Emigration (γ''_7)	0.170	0.206	0.012	0.780
Emigration (γ''_8)	0.628	0.253	0.168	0.934
Immigration (γ'_2)	0.774	0.096	0.539	0.910
Immigration (γ'_3)	0.319	0.110	0.148	0.559
Immigration (γ'_4)	0.793	0.096	0.550	0.923
Immigration (γ'_5)	0.575	0.119	0.343	0.778
Immigration (γ'_6)	0.794	0.100	0.537	0.928
Immigration (γ'_7)	0.149	0.163	0.014	0.684
Immigration (γ'_8)	0.613	0.266	0.150	0.935

Model-averaged parameters are the expected number of resightings (λ), total population size (N), apparent survival (ϕ), and two parameters for temporary emigration: the probability of transitioning from observable to unobservable (γ'') and of remaining unobservable (γ').

The point estimates of total population size (*N*) were biased low and smaller than MNA for the majority of primary occasions (Tables 2.4 – 2.5). Over both analyses, all but three of the 95% confidence intervals included MNA, but most of the point estimates had to be adjusted for MNA.

Few patterns were evident in residual plots, and most residuals appeared to be randomly distributed around zero. However, the general model and the top model had more positive than negative residuals, and large positive residuals came from two owl nests on town 78: one where owls were seen early in the season and not again until the end of the season, and one where owls were seen many times early in the season but never again later. This nest either failed or the owls moved. Abundance estimates were generally smaller than MNA from visual counts, but the 4-week apparent survival estimate of 0.500 was reasonable in comparison with the minimum estimate from visual counts of 0.466 fledged owlets per emerged owlet; of 174 owlets known alive at first emergence at 14 d on the six M-R towns, 81 owlets remained to fledge at 42 d.

Table 2.4. Abundance: Town 78. Point estimates of total population size (*N*) from the town 78 M-R analysis were biased low, and smaller than the minimum number known alive (MNA) for all but the first primary occasion, when the number of marked individuals was known and assumed to be the same as when we banded during the previous evening. The 95% confidence intervals included MNA for all but the fourth occasion, but point estimates were adjusted for MNA.

N	MNA	MARK Estimate				Adjusted Estimate
		Estimate	SE	LCI	UCI	
N_1	30	31.43	4.60	22.41	40.44	31.43
N_2	23	14.49	4.61	5.45	23.53	23
N_3	26	21.68	4.50	12.85	30.50	26
N_4	28	17.56	3.05	11.59	23.54	28
N_5	19	17.23	6.24	4.99	29.46	19
N_6	5	3.80	2.68	-1.45	9.05	5

Table 2.5. Abundance: Site-Wide Analysis. Point estimates of total population size (*N*) from the M-R analysis were biased low and smaller than the minimum number known alive (MNA) for six of the nine primary occasions. The 95% confidence intervals included MNA for all but the second and final primary occasions, but point estimates were adjusted for MNA.

N	MNA	MARK Estimate				Adjusted Estimate
		Estimate	SE	LCI	UCI	
N_1	18	15.32	3.34	8.76	21.87	18
N_2	34	20.44	3.03	14.50	26.38	34
N_3	69	63.97	11.87	40.70	87.23	69
N_4	66	69.76	11.49	47.24	92.28	69.76
N_5	28	26.82	6.08	14.91	38.73	28
N_6	59	52.94	7.90	37.46	68.42	59
N_7	26	30.40	9.20	12.37	48.44	30.40
N_8	43	46.83	11.50	24.29	69.37	46.83
N_9	18	10.74	3.23	4.41	17.07	18

Our analyses suggest that owlets in better condition (more fat and muscle over the keel) with higher weights at first capture had higher survival rates (Fig. 2.2) and were more likely to be above ground (Fig. 2.3). We did not find evidence of an age effect on survival. Apparent survival was constant through time (Tables 2.2 – 2.3): models with time effects on survival and/or time-varying covariates had weights < 5% (App. 1, Tables 2.9, 2.11). The top model in the town 78 analysis (Table 2.6) had model weight of 23.9%. The three best supported models were separated by fewer than two AICc units and collectively had 46.1% model weight. ϕ was held constant except for model 2, in which ϕ had a positive relationship with weight at first capture. Emigration parameters were held constant, except that model 3 allowed γ'' to differ from γ'. The top model in the site-wide analysis (Table 2.6) had model weight of 26.0%. The three best supported models were separated by less than one AICc unit and had 59.9% of the weight. ϕ had a positive relationship with body condition at first capture, and the third model also included a positive weight effect, although the 95% confidence intervals around the beta coefficient estimates overlapped zero. The immigration and emigration parameters were equal to one another in these models, but differed over time. The top model also included a weight effect, with birds that weighed less at first capture more likely to be underground.

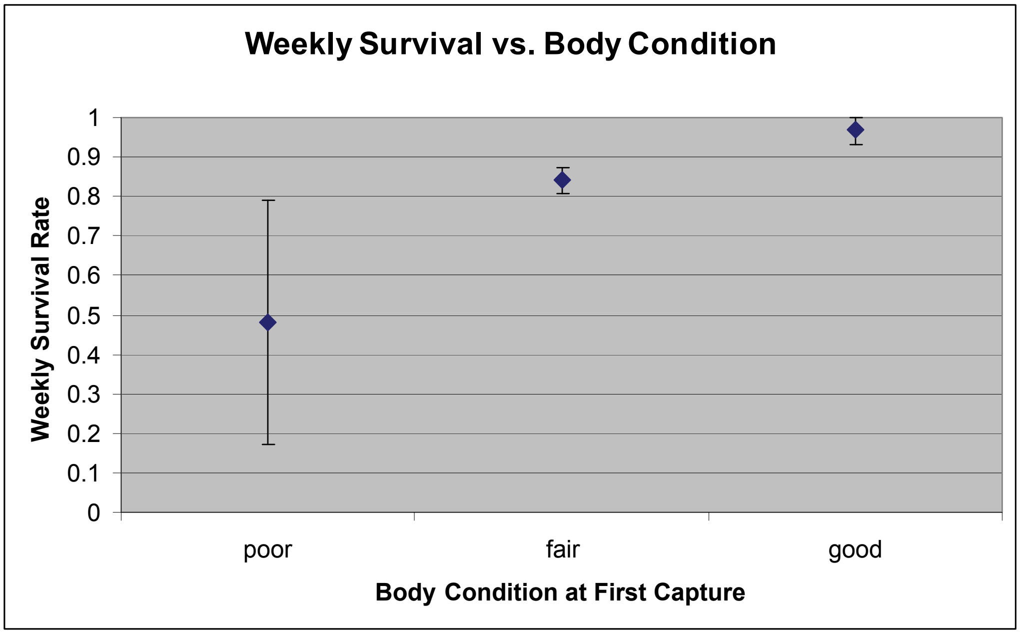

Figure 2.2. Weekly survival rate (based on the top, minimum AIC model) was higher for owlets whose body condition was higher at first capture. Body condition was quantified according to the amount of muscle and fat over the keel. Only three owlets were captured in poor condition. Bars are standard errors.

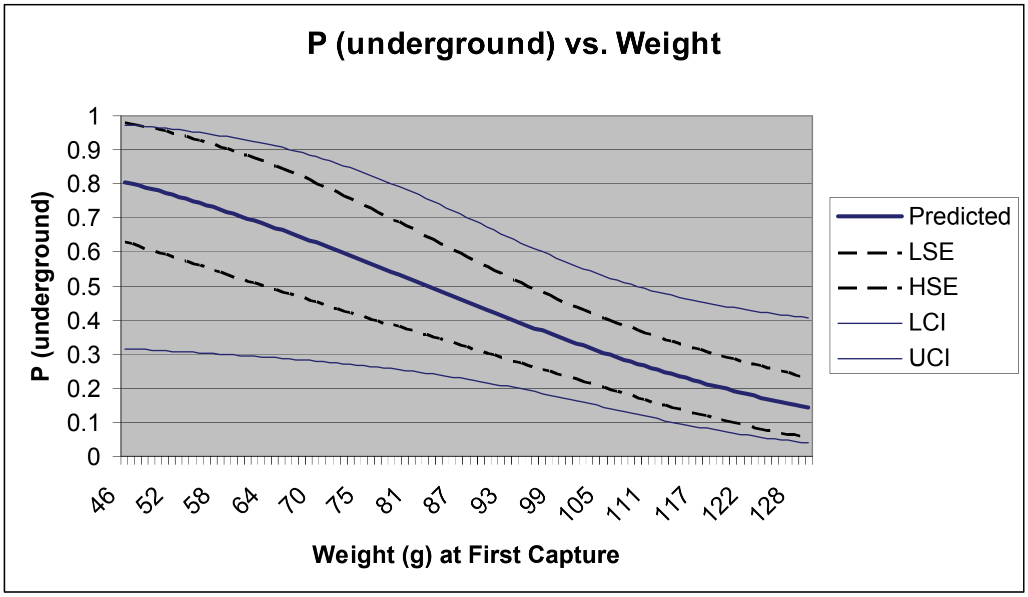

Figure 2.3. The probability of being underground (based on the top, minimum AIC model) was lower for owlets who were larger at first capture. The top model also included a time effect. These estimates apply to time interval 3 (mid-July), when abundance peaked and most banded owlets had been captured within the previous week. The trend was the same during other time intervals. Standard error and 95% confidence envelopes are shown around estimates of temporary emigration.

Table 2.6. Top Three Models. The model set was determined *a priori* (Table 2.1). The top models in each analysis had the smallest AICc and highest model weight. U was estimated separately in each primary occasion. For the site-wide analysis, α was held constant except for the first primary occasion in which only town 74, the first town where owlets were banded, was visited. All σ except the first were fixed to the σ_1 for the fully time-varying "t" model on town 78. The entire model set is included in App. 1 (Tables 2.9, 2.11).

Model	AICc	ΔAICc	Weight	Likelihood	# Par	Deviance
Town 78 Analysis						
$\{\alpha(.)\ \sigma(\text{fix})\ U(\text{t})\ \phi(.)\ \gamma''(.)=\gamma'(.)\}$	416.865	0.000	0.239	1.000	10	391.749
$\{\alpha(.)\ \sigma(\text{fix})\ U(\text{t})\ \phi(\text{weight})\ \gamma''(.)=\gamma'(.)\}$	418.403	1.538	0.111	0.463	11	390.117
$\{\alpha(.)\ \sigma(\text{fix})\ U(\text{t})\ \phi(.)\ \gamma''(.)\ \gamma'(.)\}$	418.407	1.542	0.111	0.463	11	390.121
Site-Wide Analysis						
$\{\alpha(74.)\ \sigma(\text{fix 78})\ U(\text{t})\ \phi(\text{keel})\ \gamma''(\text{t+weight})=\gamma'(\text{t+weight})\}$	919.570	0.000	0.260	1.000	23	862.530
$\{\alpha(74.)\ \sigma(\text{fix 78})\ U(\text{t})\ \phi(\text{keel})\ \gamma''(\text{t})=\gamma'(\text{t})\}$	920.418	0.849	0.170	0.654	22	866.399
$\{\alpha(74.)\ \sigma(\text{fix 78})\ U(\text{t})\ \phi(\text{keel+weight})\ \gamma''(\text{t})=\gamma'(\text{t})\}$	920.431	0.861	0.169	0.650	23	863.391

Parameters are the log transformed intercept for mean resighting rate (α), individual heterogeneity (σ), unmarked population size (U), apparent survival (ϕ), and two parameters for temporary emigration: the probability of transitioning from observable to unobservable (γ'') and of remaining unobservable (γ').

DISCUSSION

Parameter Estimation

The Poisson log-normal mark-resight model can be used to estimate abundance, apparent survival, and temporary emigration for any species where individually identifiable marking is possible and animals can be resighted. It is especially useful for situations when individual identifications are not always possible, and when the number of marks is unknown due to mortality or emigration. The assumptions for this model are the same as for Bowden's estimator (Bowden and Kufeld 1995): closure within primary intervals (no birth, death, immigration, emigration, or loss of marks), no errors in distinguishing marked from unmarked individuals, and the same resighting probabilities (independently and identically distributed) for marked and unmarked individuals.

Our results suggest that the probability of an owlet surviving for a 4 week period (the amount of time from emergence to fledging) in a relatively poor year for reproduction (Conrey Ch. 4) was 0.500 (0.079 SE). Although only apparent survival (the probability of surviving and remaining on the study area) can be estimated using this method, owlets are very unlikely to leave the survey area prior to fledging. Because owlets begin spreading beyond the nest area when they are older than 20 d, we scanned a large radius around the nest (200+ m), and do not believe that young owlets left the area we surveyed. Similarly, temporary emigration applies to owlets that stay underground in burrows throughout a survey occasion, rather than those that leave the study area entirely.

Our site-wide analysis suggested that owlets in better condition with higher weights at first capture had higher survival rates (Fig. 2.2) and were more likely to be above ground (Fig. 2.3) for the rest of the season. Apparent survival in the top model

(Table 2.6), as assessed by AICc, had a positive relationship with body condition at first capture (amount of fat and muscle over the keel). The third model, separated from the top model by < 1 AICc unit, also included a positive weight effect, although both of the 95% confidence intervals around the beta coefficient estimates overlapped zero. The top model included a weight effect on temporary emigration, with birds that weighed less at first capture more likely to be underground. Larger owlets in better condition may have higher survival because they are healthier, better fed, and better able to compete with siblings for food. They may spend more time above ground than smaller owlets, because they are better able to expend energy chasing prey and running back to burrows when threatened. We did not find evidence of an age effect on survival.

One consideration when using this method is that abundance from the M-R model can only be estimated for sites or groups of nests (for example, all the nests on one prairie dog town), because there are not enough owlets at individual nests for nest-specific parameters to be estimated. Wherever nest success or nest-specific estimates of fate or fledging success are desired, visual counts must be used. However, a comparison of MNA from visual counts to abundance estimates from the M-R model should inform researchers about the probability that visual counts fail to detect some owlets. In addition, estimates from the M-R model apply to owlets that can potentially be sighted above ground. If survival estimates for eggs or very young nestlings are desired, a video probe could be used, but some tunnels may be too long or tortuous for successful probing (Lantz et al. 2007; Conrey 2009; Lantz and Conway 2009).

Protocol Considerations

The point estimates of total population size (*N*) for owlets from the M-R analysis were biased low, and smaller than MNA from visual counts for the majority of primary occasions (Tables 2.4 – 2.5). It was reassuring in both analyses that all but three of the 95% confidence intervals included MNA, but most of the point estimates had to be adjusted for MNA. One problem we encountered was that the number and success of nests was significantly lower than in the previous or the next year, as demonstrated by our reproductive data (Conrey Ch. 4) and the Forest Service's owl counts (Humphrey and Bruce 2007). Therefore, there were fewer owlets on the town to capture and resight than in a "good" year like 2006 or 2008.

Second, many owlets tended either to be observable for almost every scan, or for no scans, so capture histories contained more zeroes than expected in a Poisson model, with a somewhat bimodal distribution (Fig. 2.4). To improve parameter estimation in the future, a second set of scans should be done 12 – 24 hours after the first scans, so that the primary interval can still be considered demographically closed. This should result in fewer sightings of zero, and more intermediate numbers of sightings for birds, particularly for birds seen in one but not both sets of scans. Another option would be altering the underlying assumption of Poisson-distributed counts during scans. An increased probability of zero is not uncommon with count data, and can be modeled with a zero-inflated Poisson distribution. A new parameter is added to model the increased zeroes using binomial probabilities. However, such a model has not been parameterized for mark-resight analysis and is not included in Program MARK.

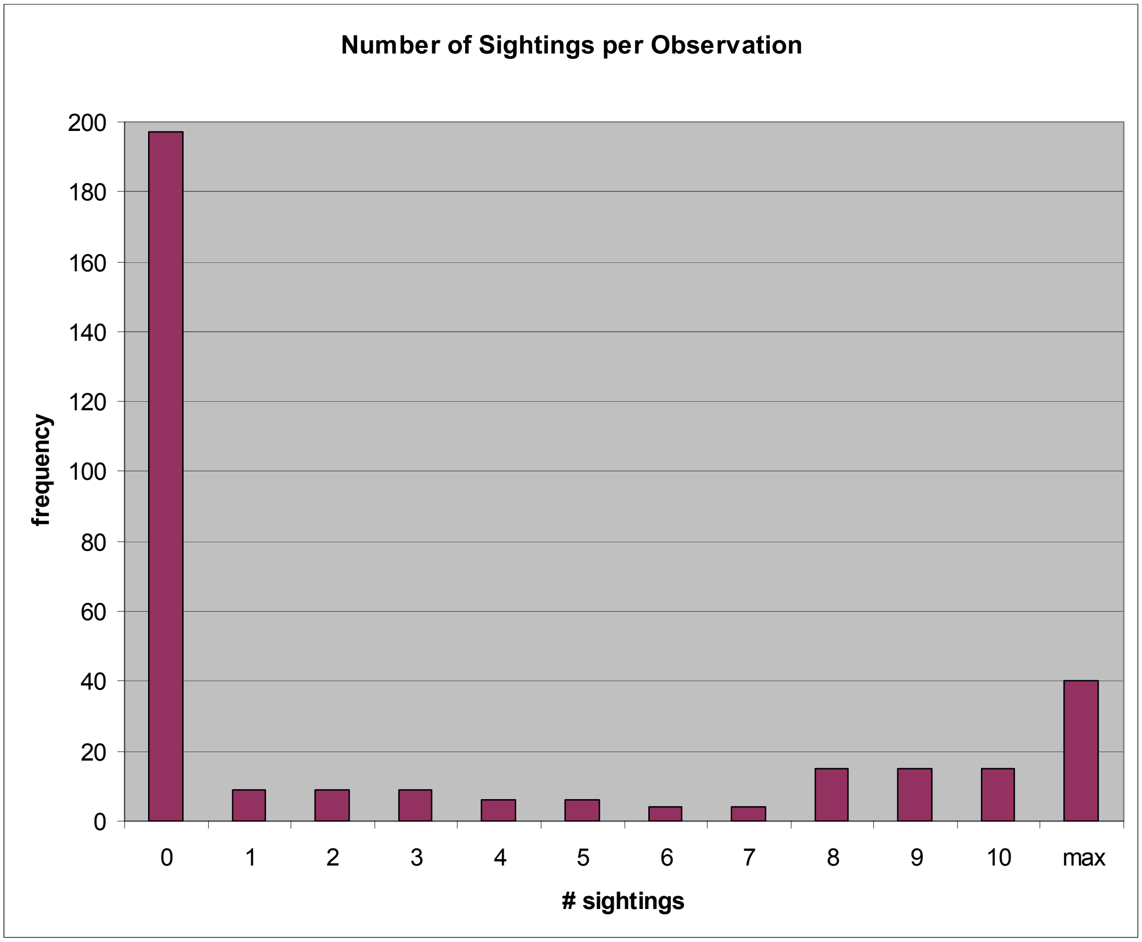

Figure 2.4. We conducted 8 – 10 scans per observation (primary occasion). By far the most common number of marked owlet sightings per observation was 0 (marked bird not seen or not identified). Most birds were sighted during every scan (maximum possible number of sightings), or not at all; during 45 observations, owlets were sighted 8 – 10 times, and for 40 of these, they were sighted during every scan. This histogram does not represent a good fit to a Poisson model. If the data were more Poisson-distributed, then the distribution would peak at λ (expected number of resightings, with range 3.75 – 7.23 in the site-wide M-R analysis), with smaller and larger values increasingly less probable.

McClintock et al. (2009) had a similar problem in their analysis of black-tailed prairie dog abundance, although it was less severe because their sample size was much larger. They used the Poisson log-normal mark-resight model to estimate abundance (but not survival or temporary emigration) over time on some of the same study areas on the PNG. Their point estimates were approximately 10% lower than estimates from other methods, which the authors attributed to more marked individuals sighted zero times than expected under a Poisson distribution. They believed that individual heterogeneity was underestimated, leading to overestimation of individual resighting rates and underestimation of abundance. Simulations with high levels of heterogeneity resulted in negative bias in abundance, but the Poisson log-normal mark-resight model still performed better than other methods. Abundance of New Zealand robins was also underestimated during one occasion when undetected heterogeneity was suspected to be high (McClintock and White 2009).

Estimation of individual heterogeneity (σ) presented a challenge in this study, and the more severe the underestimation of σ, the more severe the underestimation of abundance (N). Our estimates of MNA from visual counts allowed us to assess bias in $\hat{N}$ from the M-R model. To alleviate this problem in the analysis of town 78, all estimates of σ except the first were fixed to the σ_1 for the fully time-varying “t” model. Heterogeneity could be most accurately estimated for the first primary occasion, because the number of marks was known. For the site-wide analysis, all σ estimates except the first were fixed to the σ_1 for the fully time-varying “t” model on town 78. Heterogeneity could be most accurately estimated in town 78, because more owlets were captured here than in any other town. For the first primary occasion in town 78, $\hat{N}$ > MNA. In both analyses, when σ was not fixed in this way, bias in $\hat{N}$ was much higher.

Out of all owlet sightings, 7% (111 of 1605 sightings) were of unknown marking status. All other sightings were confirmed as either marked or unmarked birds. Because these unknown individuals could not contribute to parameter estimation, a slight underestimation of abundance may have occurred for those occasions when unknown birds were seen. However, at this low level, unknown sightings were a minor problem in comparison with the issues discussed above, including sparse data and poor fit of owlet counts to a Poisson distribution. Higher numbers of unknown sightings can be problematic; the M-R model could not be used in another study using similar methods in central eastern Colorado (Bibles 2007*a*,*b*), possibly due to lower visibility of nests or differences in techniques used by field staff (Conrey 2009). In that study, 34% (576 of 1686) of sightings were of owlets with unknown marking status (Conrey 2009).

Another complication was the difficulty in aligning the primary intervals for the six prairie dog towns, because we did not conduct resighting surveys for all towns at the same time during each week, and sometimes poor weather (wind, rain, or heat), schedule conflicts with other field crews, or shooters on towns prevented us from conducting surveys as planned. This meant that the width of the multi-town primary period (when demographic closure was assumed) was sometimes larger than the open time interval between primary occasions. This stretches the closure assumption during primary occasions; a better design would include closed primary occasions that are shorter than the open intervals between them. In addition, the smallest open interval between primary occasions when no towns were checked was 3 d, even though individual towns were surveyed just once per week. This created an apparent dichotomy between the intervals that had to be defined in Program MARK and those that existed in the field data. However, because owlets did not move between towns, they either survived or did not survive the period between weekly nest checks. This explains why survival estimates from the town 78 analysis (open interval = 1 wk) were so similar to estimates from the site-wide analysis (open interval = 3 d), and suggests that our interpretation of weekly rates was reasonable for both analyses. To address this issue in the future, all sites with marked individuals should be visited within a period of a few days, with field crews visiting other sites (where the M-R protocol is not being used) or working on other aspects of the project for the rest of the week.

Conclusion

We believe that the protocol improvements suggested here will make this M-R method useful for burrowing owls and many other species that can be marked and resighted. Abundance can be estimated throughout the breeding season. Even where visual counts are needed because nest- or litter-specific estimates are desired, this method will allow the negative bias of visual counts to be assessed. If a robust design is used, in which groups of scans are conducted over time, then apparent survival and temporary emigration can also be estimated. This is the first mark-resight model to allow estimation of apparent survival or temporary emigration. There have been few applications thus far (McClintock and White 2009), but it should prove a useful approach for many species.

Only half the owlets that emerged from burrows survived to fledging age in a year when fledging peaked during a wet month. Comparisons with other years showed that breeding success declined in wetter summers (Conrey Ch. 4). Body condition at first capture positively influenced survival, and weight at first capture positively influenced an owlet's probability of being observable above ground for the rest of the breeding season. Researchers should consider these and other sources of heterogeneity in the detectability and survival of resighted individuals, as well as the effects of annual variation on parameter estimation.

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APPENDIX 1 – MARK-RESIGHT ANALYSIS IN PROGRAM MARK

Table 2.7. Primary Occasions. Prairie dog towns were visited on nine primary occasions, but due to logistical constraints, not all towns could be visited during each time period. For the town 78 analysis, the six primary occasions were renumbered P1 – P6.

	P1	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**
Town	6/25 - 29	7/2 - 6	7/10 - 13	7/17 - 20	7/24 - 27	7/30 - 8/3	8/6 - 10	8/14 - 17	8/21 - 28
51			7/13	7/20	7/26	8/3		8/16	8/27
54				7/17	7/24	7/31	8/8	8/16	
74	6/25 - 29	7/6	7/12	7/19		7/30	8/10		
76					7/25	8/1	8/6 - 9		8/22 - 24
78		7/2 - 5	7/11	7/20		7/31 - 8/3		8/14 - 17	8/24 - 28
82			7/10	7/17	7/27		8/9		8/21 - 22

Input File: Town 78 Analysis

```
/* PAWNEE NATIONAL GRASSLAND 2007, TOWN 78*/
/* BURROWING OWLS ANALYSIS, 6 primary occasions*/
/* ID, Nest, History, 1 Group, Weight(g)*/

/*    XOOK7851*/        ..+010-0-0..      1     115;
/*    XWKW7851*/        ..+001-006..      1     114;
/*    OWXnone7852*/     +0+0-0-0-0..      1     74;
/*    WXYK7852*/        ..03-010-0..      1     110;
/*    OXYW7853*/        02-0-0-0-0..      1     95;
/*    WKOX7853*/        03-0-00203..      1     105;
/*    WWXK7853*/        02-004-0-0..      1     94;
/*    WXKY7853*/        +0-0-0-0-0..      1     85;
/*    XKWK7853*/        01-0-0-0-0..      1     95;
/*    XWOK7853*/        01-0-0-0-0..      1     78;
/*    KWXK7855*/        02-0-0-0....      1     94;
/*    KWWX7859*/        070901-0-0..      1     110;
/*    OOKX7859*/        0909-0-0-0..      1     90;
/*    XKWY7859*/        0805-0-0-0..      1     120;
/*    KYXnone7860*/     ..+0-0-0-0..      1     100;
/*    OXWO7861*/        +0-0-0-0-0..      1     85;
/*    WKXK7861*/        04-0-0-005..      1     79;
/*    XWYK7861*/        +0-0-0-0-0..      1     95;
/*    YKWX7861*/        09-0-0-0-0..      1     90;
/*    WKYX7862*/        +0-0-01001-0      1     101;
/*    WXWK7862*/        +0-010100909      1     101;
/*    XOWO7862*/        +0-010-001-0      1     89;
/*    YWOX7862*/        01-010-007-0      1     109;
/*    YWWX7863*/        +0-010-0-0..      1     118;

Unmarked Seen Group=1;
52    62    92    137   45    17;

Marked Unidentified Group=1;
31    9     27    28    3     0;

Known Marks Group=1;
20    0     0     0     0     0;
```

Figure 2.5. The input file for the town 78 analysis began with comments and descriptors, followed by data for banded individuals. The capture history consisted of two digits for each primary occasion: number of scans in which an IDd bird was sighted (e.g., 08), .. if that nest was not observed in that primary, +0 if the IDd bird was known to be present but not seen (only occurred if a bird was captured the previous night), or -0 if the IDd bird was not seen on other occasions. The single column of ones indicated that just one group was present. Weight at first capture was an individual covariate for banded owlets. The remaining rows gave the sums per primary occasion of sightings of unmarked owlets, unIDd owlets, and known marks. The number of marks was known only for the morning following the first trapping session, when all banded birds were assumed to be alive and present; otherwise, a “0” was entered for known marks. Nests were scanned via the M-R protocol following the first banding session on a particular site.

Table 2.8. Model-Averaged Parameters: Town 78. *N* was estimated separately in each primary occasion.

Model-Averaged Parameter	Estimate	SE	LCI	UCI
Unmarked Population Size (U1)	11.43	4.60	2.41	20.44
Unmarked Population Size (U2)	10.33	4.60	1.32	19.34
Unmarked Population Size (U3)	13.36	4.48	4.58	22.14
Unmarked Population Size (U4)	13.40	3.04	7.45	19.35
Unmarked Population Size (U5)	9.93	6.21	-2.23	22.10
Unmarked Population Size (U6)	2.76	2.67	-2.48	7.99
Intercept (ln) mean resighting rate (Alpha1)	1.249	0.216	0.826	1.672
Intercept (ln) mean resighting rate (Alpha2)	1.283	0.146	0.997	1.570
Intercept (ln) mean resighting rate (Alpha3)	1.288	0.133	1.028	1.549
Intercept (ln) mean resighting rate (Alpha4)	1.278	0.131	1.022	1.535
Intercept (ln) mean resighting rate (Alpha5)	1.269	0.159	0.958	1.581
Intercept (ln) mean resighting rate (Alpha6)	1.266	0.195	0.883	1.650
Individual Heterogeneity (Sigma1)	1.238	0.179	0.887	1.589
Individual Heterogeneity (Sigma2)	1.365	0.002	1.360	1.369
Individual Heterogeneity (Sigma3)	1.365	0.001	1.362	1.368
Individual Heterogeneity (Sigma4)	1.365	0.002	1.361	1.369
Individual Heterogeneity (Sigma5)	1.365	0.002	1.362	1.368
Individual Heterogeneity (Sigma6)	1.365	0.002	1.361	1.369
Expected # Sightings (Lambda1)	4.23	0.45	3.36	5.11
Expected # Sightings (Lambda2)	5.42	0.40	4.64	6.21
Expected # Sightings (Lambda3)	6.52	0.38	5.78	7.26
Expected # Sightings (Lambda4)	9.97	0.42	9.15	10.79
Expected # Sightings (Lambda5)	3.63	0.41	2.83	4.43
Expected # Sightings (Lambda6)	3.22	0.49	2.25	4.18
Total Population Size (N1)	31.43	4.60	22.41	40.44
Total Population Size (N2)	14.49	4.61	5.45	23.53
Total Population Size (N3)	21.68	4.50	12.85	30.50
Total Population Size (N4)	17.56	3.05	11.59	23.54
Total Population Size (N5)	17.23	6.24	4.99	29.46
Total Population Size (N6)	3.80	2.68	-1.45	9.05
Apparent Survival (Phi1)	0.824	0.091	0.579	0.941
Apparent Survival (Phi2)	0.818	0.096	0.558	0.941
Apparent Survival (Phi3)	0.817	0.084	0.598	0.930
Apparent Survival (Phi4)	0.823	0.082	0.606	0.934
Apparent Survival (Phi5)	0.780	0.208	0.248	0.974
Emigration (Gamma"1)	0.626	0.091	0.439	0.781
Emigration (Gamma"2)	0.625	0.091	0.437	0.782
Emigration (Gamma"3)	0.626	0.091	0.439	0.782
Emigration (Gamma"4)	0.624	0.095	0.429	0.786
Emigration (Gamma"5)	0.625	0.092	0.436	0.783
Immigration (Gamma'2)	0.590	0.133	0.330	0.808
Immigration (Gamma'3)	0.590	0.133	0.328	0.809
Immigration (Gamma'4)	0.591	0.132	0.330	0.808
Immigration (Gamma'5)	0.591	0.132	0.330	0.809

Model-averaged parameters for town 78 are the unmarked population size (*U*), log transformed intercept for mean resighting rate (α), individual heterogeneity (σ), expected number of resightings (λ), total population size (*N*), apparent survival (ϕ), and two parameters for temporary emigration: the probability of transitioning from observable to unobservable (γ'') and of remaining unobservable (γ')

Table 2.9. Model Set: Town 78 Analysis. The model set for the town 78 analysis was determined *a priori* (Table 2.1). The top model had the smallest AICc and highest model weight. *U* was estimated separately in each primary occasion. For these models, all σ except the first were fixed to the σ_1 for the fully time-varying "t" model.

Model	AICc	ΔAICc	Weight	Likelihood	# Par	Deviance
{alpha(.) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	416.865	0.000	0.239	1.000	10	391.749
{alpha(.) sigma(fix) U(t) Phi(weight) Gamma''(.)=Gamma'(.) DM logit}	418.403	1.538	0.111	0.463	11	390.117
{alpha(.) sigma(fix) U(t) Phi(.) Gamma''(.) Gamma'(.) DM logit}	418.407	1.542	0.111	0.463	11	390.121
{alpha(t1) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	419.665	2.800	0.059	0.247	11	391.379
{alpha(wind) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	419.714	2.849	0.058	0.241	11	391.429
{alpha(age2) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	419.940	3.075	0.051	0.215	11	391.654
{alpha(.) sigma(fix) U(t) Phi(age2) Gamma''(.)=Gamma'(.) DM logit}	419.983	3.118	0.050	0.210	11	391.697
{alpha(age) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	419.984	3.119	0.050	0.210	11	391.698
{alpha(weight) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	420.011	3.146	0.050	0.208	11	391.725
{alpha(temp) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	420.033	3.168	0.049	0.205	11	391.747
{alpha(T) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	420.034	3.169	0.049	0.205	11	391.748
{alpha(.) sigma(fix) U(t) Phi(t) Gamma''(.)=Gamma'(.) DM logit}	421.031	4.166	0.030	0.125	12	389.421
{alpha(t1) sigma(fix) U(t) Phi(weight) Gamma''(.)=Gamma'(.) DM logit}	421.359	4.495	0.025	0.106	12	389.750
{alpha(t1) sigma(fix) U(t) Phi(.) Gamma''(.) Gamma'(.) DM logit}	421.367	4.502	0.025	0.105	12	389.757
{alpha(.) sigma(fix) U(t) Phi(T2) Gamma''(.)=Gamma'(.) DM logit}	422.131	5.266	0.017	0.072	12	390.521
{alpha(T2) sigma(fix) U(t) Phi(.) Gamma''(.)=Gamma'(.) DM logit}	422.840	5.975	0.012	0.050	12	391.230
{alpha(.) sigma(fix) U(t) Phi(t) Gamma''(.) Gamma'(.) DM logit}	423.174	6.309	0.010	0.043	13	388.074
{alpha(.) sigma(fix) U(t) Phi(.) Gamma''(t) Gamma'(t) DM logit}	426.635	9.770	0.002	0.008	16	379.932
{alpha(.) sigma(fix) U(t) Phi(t) Gamma''(t) Gamma'(t) DM logit}	429.898	13.033	0.000	0.002	17	378.898
{alpha(t) sigma(fix) U(t) Phi(.) Gamma''(.) Gamma'(.) PIM logit}	436.149	19.284	0.000	0.000	16	389.447
{alpha(t) sigma(t) U(t) Phi(t) Gamma''(t) Gamma'(t) PIM logit}	439.804	22.940	0.000	0.000	25	343.376
{alpha(t) sigma(fix) U(t) Phi(.) Gamma''(t) Gamma'(t) PIM logit}	444.619	27.754	0.000	0.000	20	379.165
{alpha(t) sigma(fix) U(t) Phi(t) Gamma''(.) Gamma'(.) PIM logit}	446.213	29.348	0.000	0.000	19	385.860
{alpha(t) sigma(fix) U(t) Phi(t) Gamma''(t) Gamma'(t) DM logit}	454.708	37.843	0.000	0.000	22	378.063
{alpha(t) sigma(t) U(t) Phi(t) Gamma''(t) Gamma'(t) PIM logit}	464.336	47.471	0.000	0.000	28	343.376
{alpha(.) sigma(fix) U(t) Phi(.) DM logit}	526.126	109.261	0.000	0.000	9	504.035

Parameters are the log transformed intercept for mean resighting rate (α), individual heterogeneity (σ), unmarked population size (U), apparent survival (ϕ), and two parameters for temporary emigration: the probability of transitioning from observable to unobservable (γ'') and of remaining unobservable (γ').

Input File: Site-Wide Analysis

```
/* PAWNEE NATIONAL GRASSLAND 2007*/
/* BURROWING OWLS ANALYSIS, 9 primary occasions*/
/* ID, Nest, History, Prairie Dog Towns are indiv covariates, Weight(g), Keel(body condition)*/
/* 1 Group*/
/* Following column of 1s, next 6 columns are for town 51, 54, 74, 76, 78, 82*/
/* Keel 0 = poor, 1 = fair, 2 = good*/

/*     WOXY5153*/          ....0803-008..-0-0  1      1      0      0      0      0      0      117    1;
/*     XOOW5153*/          ....08-0-0-0..-0-0  1      1      0      0      0      0      0      99     1;
/*     KKXK5158*/          ......090802..05..  1      1      0      0      0      0      0      101    1;
/*     OXWW5158*/          ....05090709..05..  1      1      0      0      0      0      0      117    1;
/*     XKWO5158*/          ......0907-0..06..  1      1      0      0      0      0      0      115    1;
/*     WXKK5160*/          ....+006-0-0..-0..  1      1      0      0      0      0      0      84     1;
/*     XOOO5160*/          ....+009-0-0..-0..  1      1      0      0      0      0      0      98     1;
/*     OOXW5451*/          ......+01008-008..  1      0      1      0      0      0      0      117    2;
/*     WXOY5452*/          ........090810....  1      0      1      0      0      0      0      117    2;
/*     OKWX5454*/          ......03-0-0-0....  1      0      1      0      0      0      0      106    1;
/*     OWXO5454*/          ......03+0-0-0....  1      0      1      0      0      0      0      117    1;
/*     WYYX5458*/          ........+0-0-0-0..  1      0      1      0      0      0      0      130    2;
/*     OXKW7451*/          03-0-0-0..-0-0....  1      0      0      1      0      0      0      55     1;
/*     WXYW7451*/          ..+0-010..-0-0....  1      0      0      1      0      0      0      124    1;
/*     XWOW7451*/          03-0-0-0..-0-0....  1      0      0      1      0      0      0      75     1;
/*     KWKX7455*/          ..+0-010..-008....  1      0      0      1      0      0      0      124    1;
/*     WOWX7455*/          ..+0-0-0..-0-0....  1      0      0      1      0      0      0      119    1;
/*     XKKK7455*/          02-0-010..-0-0....  1      0      0      1      0      0      0      85     1;
/*     KOOX7457*/          08-0-010..-008....  1      0      0      1      0      0      0      85     1;
/*     WWWX7457*/          +0................  1      0      0      1      0      0      0      75     1;
/*     WXKW7457*/          08-0-0-0..-0-0....  1      0      0      1      0      0      0      113    1;
/*     YWXK7457*/          +0-0-0-0..-0-0....  1      0      0      1      0      0      0      46     1;
/*     YXWW7457*/          08-00410..-0-0....  1      0      0      1      0      0      0      85     1;
/*     KXKK7655*/          ........04-0-0..-0  1      0      0      0      1      0      0      103    1;
/*     XKWW7655*/          ........04-002..-0  1      0      0      0      1      0      0      94     1;
/*     XWWO7655*/          ........0403-0..-0  1      0      0      0      1      0      0      97     1;
/*     XOOK7851*/          ....+010..-0..-0..  1      0      0      0      0      1      0      115    1;
/*     XWKW7851*/          ....+001..-0..06..  1      0      0      0      0      1      0      114    1;
/*     OWXnone7852*/       ..+0+0-0..-0..-0..  1      0      0      0      0      1      0      74     1;
/*     WXYK7852*/          ....03-0..10..-0..  1      0      0      0      0      1      0      110    2;
/*     OXYW7853*/          ..02-0-0..-0..-0..  1      0      0      0      0      1      0      95     0;
/*     WKOX7853*/          ..03-0-0..02..03..  1      0      0      0      0      1      0      105    1;
/*     WWXK7853*/          ..02-004..-0..-0..  1      0      0      0      0      1      0      94     1;
/*     WXKY7853*/          ..+0-0-0..-0..-0..  1      0      0      0      0      1      0      85     1;
```

```
/*     XKWK7853*/           ..01-0-0..-0..-0..  1      0      0      0      0      1      0      95     1;
/*     XWOK7853*/           ..01-0-0..-0..-0..  1      0      0      0      0      1      0      78     1;
/*     KWXK7855*/           ..02-0-0..-0......  1      0      0      0      0      1      0      94     1;
/*     KWWX7859*/           ..070901..-0..-0..  1      0      0      0      0      1      0      110    2;
/*     OOKX7859*/           ..0909-0..-0..-0..  1      0      0      0      0      1      0      90     1;
/*     XKWY7859*/           ..0805-0..-0..-0..  1      0      0      0      0      1      0      120    1;
/*     KYXnone7860*/        ....+0-0..-0..-0..  1      0      0      0      0      1      0      100    1;
/*     OXWO7861*/           ..+0-0-0..-0..-0..  1      0      0      0      0      1      0      85     1;
/*     WKXK7861*/           ..04-0-0..-0..05..  1      0      0      0      0      1      0      79     1;
/*     XWYK7861*/           ..+0-0-0..-0..-0..  1      0      0      0      0      1      0      95     1;
/*     YKWX7861*/           ..09-0-0..-0..-0..  1      0      0      0      0      1      0      90     1;
/*     WKYX7862*/           ..+0-0-0..10..01-0  1      0      0      0      0      1      0      101    2;
/*     WXWK7862*/           ..+0-010..10..0909  1      0      0      0      0      1      0      101    1;
/*     XOWO7862*/           ..+0-010..-0..01-0  1      0      0      0      0      1      0      89     1;
/*     YWOX7862*/           ..01-010..-0..07-0  1      0      0      0      0      1      0      109    1;
/*     YWWX7863*/           ..+0-010..-0..-0..  1      0      0      0      0      1      0      118    1;
/*     WXOK8251*/           ....09-0-0..-0....  1      0      0      0      0      0      1      112    1;
/*     OOXO8252*/           ....+0-0-0..-0..-0  1      0      0      0      0      0      1      114    1;
/*     WOXK8252*/           ....+0-0-0..-0..-0  1      0      0      0      0      0      1      103    1;
/*     WOOX8253*/           ............09..-0  1      0      0      0      0      0      1      92     0;
/*     WWKX8253*/           ............-0..-0  1      0      0      0      0      0      1      105    0;
/*     WKKX8254*/           ......+0-0..-0..01  1      0      0      0      0      0      1      112    1;
/*     WWXY8254*/           ......+0-0..-0..-0  1      0      0      0      0      0      1      68     1;
/*     KOXK8255*/           ....+002-0..-0..-0  1      0      0      0      0      0      1      109    1;
/*     WYXO8255*/           ....+0-0-0..-0..-0  1      0      0      0      0      0      1      117    1;
/*     XOWW8256*/           ....0901-0..-0..-0  1      0      0      0      0      0      1      124    1;

Unmarked Seen Group=1;
29     61     268    218    106    290    111    147    65;

Marked Unidentified Group=1;
0      50     18     35     19     37     5      9      8;

Known Marks Group=1;
8      0      0      0      0      0      0      0      0;
```

Figure 2.6. The input file for the site-wide analysis (towns combined into one group) began with comments and descriptors, followed by data for banded individuals. The capture history consisted of two digits for each primary occasion: number of scans in which an IDd bird was sighted (e.g., 08), .. if that nest was not observed in that primary, +0 if the IDd bird was known to be present but not seen (only occurred if a bird was captured the previous night), or -0 if the IDd bird was not seen on other occasions. Following a column of ones for the single group, the next six

columns included the six towns as individual covariates in binary fashion (e.g., 1 if town 51, 0 otherwise). Weight and body condition (poor, fair, good) based on the keel at first capture were also individual covariates for banded owlets. The remaining rows gave the sums per primary occasion of sightings of unmarked owlets, unIDd owlets, and known marks. The number of marks was known only for the morning following the first trapping session, when all banded birds were assumed to be alive and present; otherwise, a “0” was entered for known marks. Nests were scanned via the M-R protocol following the first banding session on a particular site.

Table 2.10. Model-Averaged Parameters: Site-Wide Analysis. *N* was estimated separately in each primary occasion.

Model-Averaged Parameter	Estimate	SE	LCI	UCI
Unmarked Population Size (U1)	7.32	3.34	0.76	13.87
Unmarked Population Size (U2)	7.91	3.02	2.00	13.82
Unmarked Population Size (U3)	53.53	11.85	30.30	76.75
Unmarked Population Size (U4)	45.74	11.45	23.31	68.18
Unmarked Population Size (U5)	18.46	6.06	6.58	30.35
Unmarked Population Size (U6)	42.50	7.88	27.05	57.94
Unmarked Population Size (U7)	25.18	9.19	7.16	43.20
Unmarked Population Size (U8)	35.34	11.48	12.84	57.85
Unmarked Population Size (U9)	8.65	3.23	2.32	14.98
Intercept (ln) mean resighting rate (Alpha1)	2.957	1.207	0.592	5.323
Intercept (ln) mean resighting rate (Alpha2)	1.278	0.678	-0.052	2.608
Intercept (ln) mean resighting rate (Alpha3)	1.278	0.678	-0.052	2.608
Intercept (ln) mean resighting rate (Alpha4)	1.278	0.678	-0.052	2.608
Intercept (ln) mean resighting rate (Alpha5)	1.278	0.678	-0.052	2.608
Intercept (ln) mean resighting rate (Alpha6)	1.278	0.678	-0.052	2.608
Intercept (ln) mean resighting rate (Alpha7)	1.278	0.678	-0.052	2.608
Intercept (ln) mean resighting rate (Alpha8)	1.278	0.678	-0.052	2.608
Intercept (ln) mean resighting rate (Alpha9)	1.278	0.678	-0.052	2.608
Individual Heterogeneity (Sigma1)	0.686	0.283	0.143	0.966
Individual Heterogeneity (Sigma2)	1.365	0.000	1.365	1.365
Individual Heterogeneity (Sigma3)	1.365	0.000	1.365	1.365
Individual Heterogeneity (Sigma4)	1.365	0.000	1.365	1.365
Individual Heterogeneity (Sigma5)	1.365	0.000	1.365	1.365
Individual Heterogeneity (Sigma6)	1.365	0.000	1.365	1.365
Individual Heterogeneity (Sigma7)	1.365	0.000	1.365	1.365
Individual Heterogeneity (Sigma8)	1.365	0.000	1.365	1.365
Individual Heterogeneity (Sigma9)	1.365	0.000	1.365	1.365
Expected # Sightings (Lambda1)	3.75	1.20	1.40	6.10
Expected # Sightings (Lambda2)	7.23	1.73	3.83	10.63
Expected # Sightings (Lambda3)	4.97	1.73	1.58	8.35
Expected # Sightings (Lambda4)	4.70	1.73	1.32	8.08
Expected # Sightings (Lambda5)	5.52	1.73	2.13	8.91
Expected # Sightings (Lambda6)	6.79	1.73	3.39	10.18
Expected # Sightings (Lambda7)	4.20	1.72	0.82	7.58
Expected # Sightings (Lambda8)	4.03	1.72	0.65	7.41
Expected # Sightings (Lambda9)	7.07	1.73	3.68	10.47
Total Population Size (N1)	15.32	3.34	8.76	21.87
Total Population Size (N2)	20.44	3.03	14.50	26.38
Total Population Size (N3)	63.97	11.87	40.70	87.23
Total Population Size (N4)	69.76	11.49	47.24	92.28
Total Population Size (N5)	26.82	6.08	14.91	38.73
Total Population Size (N6)	52.94	7.90	37.46	68.42
Total Population Size (N7)	30.40	9.20	12.37	48.44
Total Population Size (N8)	46.83	11.50	24.29	69.37
Total Population Size (N9)	10.74	3.23	4.41	17.07

Apparent Survival (Phi1)	0.827	0.055	0.692	0.910
Apparent Survival (Phi2)	0.833	0.037	0.747	0.894
Apparent Survival (Phi3)	0.834	0.036	0.750	0.893
Apparent Survival (Phi4)	0.838	0.033	0.764	0.893
Apparent Survival (Phi5)	0.842	0.037	0.757	0.902
Apparent Survival (Phi6)	0.845	0.041	0.747	0.910
Apparent Survival (Phi7)	0.848	0.046	0.733	0.919
Apparent Survival (Phi8)	0.849	0.049	0.727	0.923
Emigration (Gamma"1)	1.000	0.004	0.993	1.007
Emigration (Gamma"2)	0.775	0.092	0.551	0.906
Emigration (Gamma"3)	0.317	0.110	0.146	0.558
Emigration (Gamma"4)	0.786	0.093	0.553	0.916
Emigration (Gamma"5)	0.569	0.124	0.329	0.780
Emigration (Gamma"6)	0.798	0.099	0.543	0.929
Emigration (Gamma"7)	0.170	0.206	0.012	0.780
Emigration (Gamma"8)	0.628	0.253	0.168	0.934
Immigration (Gamma'2)	0.774	0.096	0.539	0.910
Immigration (Gamma'3)	0.319	0.110	0.148	0.559
Immigration (Gamma'4)	0.793	0.096	0.550	0.923
Immigration (Gamma'5)	0.575	0.119	0.343	0.778
Immigration (Gamma'6)	0.794	0.100	0.537	0.928
Immigration (Gamma'7)	0.149	0.163	0.014	0.684
Immigration (Gamma'8)	0.613	0.266	0.150	0.935

Table 2.11. Model Set: Site-Wide Analysis. The model set for the site-wide analysis was determined *a priori* (Table 2.1). The top model had the smallest AICc and highest model weight. *U* was estimated separately in each primary occasion. Most models held α constant except for the first primary occasion in which only town 74, the first town where owlets were banded, was visited. For these models, all σ except the first were fixed to the σ_1 for the fully time-varying "t" model on town 78.

Model	AICc	ΔAICc	Weight	Likelihood	# Par	Deviance
{Phi(keel) gamma'(t+weight)=gamma"(t+weight) alpha(74 .) sigma(fix 78) U(t)}	919.570	0.000	0.260	1.000	23	862.530
{Phi(keel) gamma'(t)=gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	920.418	0.849	0.170	0.654	22	866.399
{Phi(keel+weight) gamma'(t)=gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	920.431	0.861	0.169	0.650	23	863.391
{Phi(keel+weight) gamma'(t+weight)=gamma"(t+weight) alpha(74 .) sigma(fix 78) U(t)}	922.038	2.468	0.076	0.291	24	861.916
{Phi(weight) gamma'(t)=gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	922.038	2.469	0.076	0.291	22	868.018
{Phi(.) gamma'(t)=gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	922.523	2.953	0.059	0.228	21	871.464
{Phi(keel) gamma'(t+keel)=gamma"(t+keel) alpha(74 .) sigma(fix 78) U(t)}	922.663	3.094	0.055	0.213	23	865.623
{Phi(age2) gamma'(t)=gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	922.903	3.333	0.049	0.189	22	868.883
{Phi(age) gamma'(t)=gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	923.037	3.467	0.046	0.177	22	869.017
{Phi(.) gamma'(t) gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	924.418	4.849	0.023	0.089	24	864.297
{Phi(.) gamma'(t)=gamma"(t) alpha(74 weight) sigma(fix 78) U(t)}	925.484	5.914	0.014	0.052	22	871.464
{Phi(weight) gamma'(t+weight)=gamma"(t+weight) alpha(74 .) sigma(fix 78) U(t)}	929.014	9.444	0.002	0.009	22	874.994
{Phi(Town) gamma'(t)=gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	931.963	12.393	0.001	0.002	26	865.489
{Phi(.) gamma'(t)=gamma"(t) alpha(74 Town) sigma(fix 78) U(t)}	935.537	15.967	0.000	0.000	26	869.062
{Phi(.) gamma'(.)=gamma"(.) alpha(74 .) sigma(fix 78) U(t)}	936.003	16.434	0.000	0.000	14	904.150
{Phi(.) gamma'(t) gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	937.392	17.822	0.000	0.000	28	864.297
{Phi(.) gamma'(.) gamma"(.) alpha(74 .) sigma(fix 78) U(t)}	937.900	18.330	0.000	0.000	15	903.456
{Phi(.) gamma'(t)=gamma"(t) alpha(t) sigma(fix 78) U(t)}	946.548	26.978	0.000	0.000	29	870.037
{Phi(t) gamma'(.) gamma"(.) alpha(74 .) sigma(fix 78) U(t)}	949.168	29.599	0.000	0.000	22	895.148
{Phi(t) gamma'(t) gamma"(t) alpha(74 .) sigma(fix 78) U(t)}	957.936	38.366	0.000	0.000	35	859.299
{Phi(t) gamma'(t) gamma"(t) alpha(t) sigma(fix 78) U(t)}	991.570	72.000	0.000	0.000	42	862.977

Parameters are the log transformed intercept for mean resighting rate (α), individual heterogeneity (σ), unmarked population size (*U*), apparent survival (ϕ), and two parameters for temporary emigration: the probability of transitioning from observable to unobservable (γ'') and of remaining unobservable (γ').

CHAPTER 3

BURROWING OWL DIET CORRELATES WITH RAINFALL AND BREEDING SUCCESS BUT NOT PLAGUE OUTBREAKS

ABSTRACT

Food supply often influences breeding success in predators. Burrowing owls (*Athene cunicularia*) on the shortgrass steppe of northern Colorado nest in burrows dug by black-tailed prairie dogs (*Cynomys ludovicianus*), who live in colonies periodically extirpated by plague outbreaks caused by the bacterium *Yersinia pestis*. Our objectives were to quantify prey use of burrowing owls, to examine the effects of precipitation, nest density, and plague on prey use, and to determine whether prey composition influenced nest or fledging success. We monitored 296 nests from 2005 – 2007, identified prey items from regurgitated pellets and prey remains, and analyzed prey species composition using multivariate tools. Burrowing owls ate a large variety of prey dominated by beetles, grasshoppers, ants, rodents, and songbirds, in that order. Insects comprised 95% of their diet by number, but only 11% by biomass. The largest differences in prey composition were associated with year, rainfall, nest success, and fledging success. Owls in the driest year of our study and those at successful and very productive nests ate fewer birds and more mammals. Grasshopper consumption was associated with dry weather, while scarabs and ants were indicators of wetter summers. Consumption of some, but not all, vertebrates declined at high nest densities. Owl diet was unchanged by plague outbreaks,

except that several bird species were less commonly eaten following epizootics. Based on habitat associations of the most commonly eaten rodents, this suggests that burrowing owls often forage from roadsides and fencerows outside of prairie dog towns, making town-level differences less relevant to owl diets.

INTRODUCTION

Prey availability and selection influence breeding success in predators, and predator diets may reflect environmental factors such as precipitation, temperature, and the presence of other predators or species that alter habitat. Food supply may influence the weight and survival of young, with food-stressed individuals becoming less vigilant and more likely to be predated (Newton 1998). Larger prey items may be associated with higher nest success (White 1996). Bad weather limits prey availability, decreases foraging efficiency, and can reduce nest success and survival in raptors (Village 1986; Steenhof et al. 1997).

For the burrowing owl (*Athene cunicularia hypugaea*), a small ground-dwelling owl of the western American prairies, the effects of dietary composition on nest success (proportion of nests fledging at least one juvenile) and productivity (number of fledglings per nest) were unknown. Previous studies produced contradictory results. Ronan (2002) found increased productivity for successful nests with higher rodent consumption, but there was no effect on nest success or productivity when all nests, failed and successful, were combined. Woodard (2002) observed a marginal decline in productivity for all nests as prey species richness and owl predation of vertebrates increased, but no relationship between diet and productivity for successful nests.

The effects of factors such as rainfall, nest density, and plague epizootics on diets of burrowing owls living on black-tailed prairie dog (*Cynomys ludovicianus*) towns were also unknown. However, we suspected that variation in these factors influenced breeding success (Conrey Ch. 4), and that these responses might be mediated through dietary changes. For example, precipitation is considered to be the most important environmental factor governing ecology on the shortgrass steppe (Lauenroth and Sala 1992). Ronan (2002) reported high variation in rainfall during a 3-year study in California, and found that owl breeding success was highest in the driest year that followed a very wet year. Owlet mortality may increase during periods of heavy rain, especially when rainfall lasts for several days (Wellicome 2000; Griebel and Savidge 2003). Although some prey populations may eventually respond positively to increased rainfall, burrowing owls curtail their foraging in wet weather. High density of nests has led to decreased nest success in some (Griebel and Savidge 2007) but not all studies (Rosenberg and Haley 2004). A decline in nest success may result from competition for food or satellite burrows (used for rest or refuge) or other factors related to nest predators or parasites. To our knowledge, no one has studied the effects of plague on nest success, productivity, or owl diets. Many studies have found that owls prefer active to inactive prairie dog towns (e.g., Butts and Lewis 1982; Toombs 1997; Sidle et al. 2001; Tipton et al. 2008), but the effects of extirpation and gradual recovery of prairie dogs, with the accompanying changes to vegetation and potential prey species, are unknown.

In the northern United States and Canada, most burrowing owl populations are migratory, nesting in burrows dug by mammals such as prairie dogs and ground squirrels (Haug et al. 1993). Black-tailed prairie dog burrows on our site were used as nests and satellite burrows, and mounds were used as perches. Plague, a disease caused by the introduced bacterium *Yersinia pestis*, is lethal to prairie dogs and was first reported in northern Colorado ~ 1948 (Ecke and Johnson 1952). Plague does not make owls sick, but they may be affected as unmaintained burrows collapse and become uninhabitable, vegetation grows taller, and the anti-predator benefits of prairie dog association are lost. These may include increased visibility from trimming of vegetation, alarm calling, and providing an abundant alternate prey source (Hoogland 1995). Burrowing owls are widely distributed on the prairies of North, Central, and South America, but they are a declining and protected species in many areas and are a state-listed threatened species in Colorado (Colorado Division of Wildlife 2007).

Even without direct observation of owl predation, diets can be studied by examining undigestible, identifiable prey materials regurgitated as pellets. Bones, teeth, hair, feathers, claws, talons, and chitin (insect exoskeletons) are often identifiable in owl pellets, and unconsumed prey remains such as tails and feathers are left at nests and roosts. Quantification of prey items from pellets is usually a reliable reflection of prey consumption (Glading et al. 1943; Mikkola 1983). Dietary studies of burrowing owls throughout North and South America have found them to be generalists, consuming a wide variety of invertebrates and vertebrates (Marti 1974; Gleason and Craig 1979; Grimm et al. 1985; MacCracken et al. 1985; Thompson and Anderson 1988; Schmutz et al. 1991; Green et al. 1993; Plumpton and Lutz 1993; Wiley 1998; Woodard 2002; Arana et al. 2006; Littles et al. 2007), with insects typically the most frequently consumed but rodents providing greater biomass. Nesting burrowing owl males typically hunt small mammals during crepuscular periods, while both adults and juveniles hunt insects during the day (Poulin and Todd 2006). Ground foraging (running after and pouncing on prey) is the most common hunting strategy used by burrowing owls, but owls also forage from perches and from the air (Thompson and Anderson 1988).

Our first objective was to quantify prey use of burrowing owls on the Pawnee National Grassland (PNG). Burrowing owl diet in this area was described by Marti (1974) and Woodard (2002), but prey use may change from year to year because of variation in rainfall, plague, or other factors. We examined longer term trends by comparison to these previous studies from 1967 – 1969 and 2000. Our second objective was to examine the effects of year, precipitation, nest density, and plague on prey use, and to determine whether prey composition influenced nest or fledging success. Previous studies of burrowing owl diet have not taken a multivariate approach to testing ecological hypotheses. We tested the following hypotheses:

1. Owl prey use will vary among years, with a proportionally lower small mammal component in 2007, which had heavy summer rains.
2. Owl prey use will vary among prairie dog towns with different levels of prairie dog activity and time since plague. After plague epizootics, we expected higher use of prey such as kangaroo rats that are not typically found on prairie dog towns.
3. Owl prey use will vary according to the density of owl nests, with fewer large prey items where nest density is high.
4. Successful nests, particularly those with high productivity (at least four fledglings), will use a higher proportion of vertebrate prey, especially rodents.

One rationale for our first hypothesis (H1) is that prey populations fluctuate over time, and species that consume seeds and vegetation or use thick vegetation as refuge should respond to variable precipitation. In addition, fewer small mammals were caught in 2007, with flooding perhaps partially responsible for the decline (Lindquist pers. comm.; Stapp pers. comm.). A change in prey availability may lead to changes in prey use. Another rationale for H1 is that burrowing owls and other raptors may curtail foraging activity in wet weather (Village 1986; Steenhof et al. 1997; Wellicome 2000; Griebel and Savidge 2003). H2 follows from differences in vegetation (Hardwicke 2006; Hartley 2006; Hartley et al. 2009) and prey communities (Stapp 1996; Bangert and Slobodchikoff 2006; Stapp 2007; Stapp et al. 2008) among active prairie dog towns, inactive towns, and uncolonized prairie, as well as the changes that follow plague epizootics. We observed variable regrowth of vegetation following plague events, which appeared to depend on rainfall and topography (microclimate). These changes, plus the heterogeneity resulting from prairie dog recolonization of small patches of former towns and resumed digging and clipping of vegetation, might lead to variation in owl diets. Prey species like kangaroo rats that are typically uncommon on active towns might become more abundant following epizootics. Competition among owl pairs for food might limit the availability of some prey items in high density areas (H3). H4 follows from the relatively high individual biomass of rodents; a large ratio of nutritional benefit to foraging effort (MacArthur and Pianka 1966) might lead to healthier nestlings and higher breeding success (White 1996; Newton 1998; Ronan 2002).

METHODS

Study Site

Our study site (Fig. 3.1) on the Pawnee National Grassland (PNG) is located in the shortgrass steppe (SGS) of north central Colorado (Weld County). The SGS covers the central and southern Great Plains, the driest and warmest part of America's central grasslands (Lauenroth and Burke 1995; Pielke and Doesken 2008). The area managed by the USDA Forest Service PNG consists of 78,128 ha spread over a larger 50 x 100 km region with a patchwork of public and private ownership. We worked mainly in the northwestern PNG, which has mean elevation of 1650 m and mean annual precipitation of 321 mm, with > 70% of this falling as rain from April – September (National Climatic Data Center 2002; Pielke and Doesken 2008). The amount, timing, and intensity of precipitation are the most important factors in determining the ecology of the SGS (Lauenroth and Sala 1992). Most precipitation events on the PNG are small, with much of the water lost to evapotranspiration (Sala et al. 1992; Lauenroth and Bradford 2006). More than 80% of the PNG is upland steppe habitat (Hazlett 1998). The two dominant species are perennial C_4 warm-season grasses: blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*). Other common species are prickly-pear cactus (*Opuntia polyacantha*) and two dwarf shrubs: rabbitbrush (*Chrysothamnus nauseosa*) and saltbush (*Atriplex canescens*) (Lauenroth 2008).

Livestock grazing (mostly cattle) is the dominant land use across the PNG, and cattle were common on our study areas. Bird-watching and recreational shooting are also common on the PNG. Recreational shooting of legal and illegal targets occurred throughout the study period, and an 8.5-month open season (mid-June through February annually) on prairie dogs was reinstituted in June 2007 after a six-year moratorium. Extensive shooting occurred on several easily accessible towns, especially towns 51 and 78, with moderate shooting on all towns near gravel roads open to the public, and very little shooting on more isolated towns.

In a state-wide survey of Colorado, 80% of burrowing owl locations were on prairie dog colonies, and 24% of locations were in Weld County (VerCauteren et al. 2001). Burrowing owl occupancy in Colorado was highest on active prairie dog towns, followed by inactive towns, and all towns had much higher occupancy than grassland or dryland agriculture (Tipton et al. 2008). During three surveys of nine randomly-selected quarter sections (64.75 ha), we found only one nest that was not on a prairie dog town; another two off-town nests were discovered by chance. This compares to 320 nests located on prairie dog towns, which have been mapped by the Forest Service since 1981. The area occupied by these towns has increased since 1981 with an exponential increase since the mid-1990s. Declines in area occupied have occurred during recent plague epizootics, but due to rapid recolonization and the colonization of new towns, the total area occupied has remained around 1 – 2% of the PNG.

Compared to adjacent uncolonized prairie, PNG prairie dog towns have more forbs, flowers, pollinator visits, and bare ground (Hardwicke 2006; Hartley 2006; Hartley et al. 2009). Total plant biomass is lower on older towns, and both young (< 7 yrs) and old towns have reduced grass biomass and a trend toward increasing forb biomass. Extirpated towns have similar plant biomass to uncolonized prairie (Hartley 2006; Hartley et al. 2009). Animal species associated with prairie dog towns include burrowing owls, mountain plovers (*Charadrius montanus*: Dinsmore et al. 2005; Dreitz et al. 2005;

Tipton et al. 2008), horned larks (*Eremophila alpestris*: Stapp et al. 2008), lesser earless lizards (*Holbrookia maculata*: Kretzer and Cully 2001), northern grasshopper mice (*Onychomys leucogaster*: Stapp et al. 2008), and desert cottontails (*Sylvilagus audubonii*: Stapp et al. 2008). Predator species including coyotes (*Canis latrans*), swift fox (*Vulpes velox*), and badgers (*Taxidea taxus*) often hunt on prairie dog towns (Stapp et al. 2008). We also regularly observed Swainson's hawks (*Buteo swainsoni*), Northern harriers (*Circus cyaneus*), and prairie falcons (*Falco mexicanus*) on towns, plus the occasional golden eagle (*Aquila chrysaetos*) and ferruginous hawk (*Buteo regalis*).

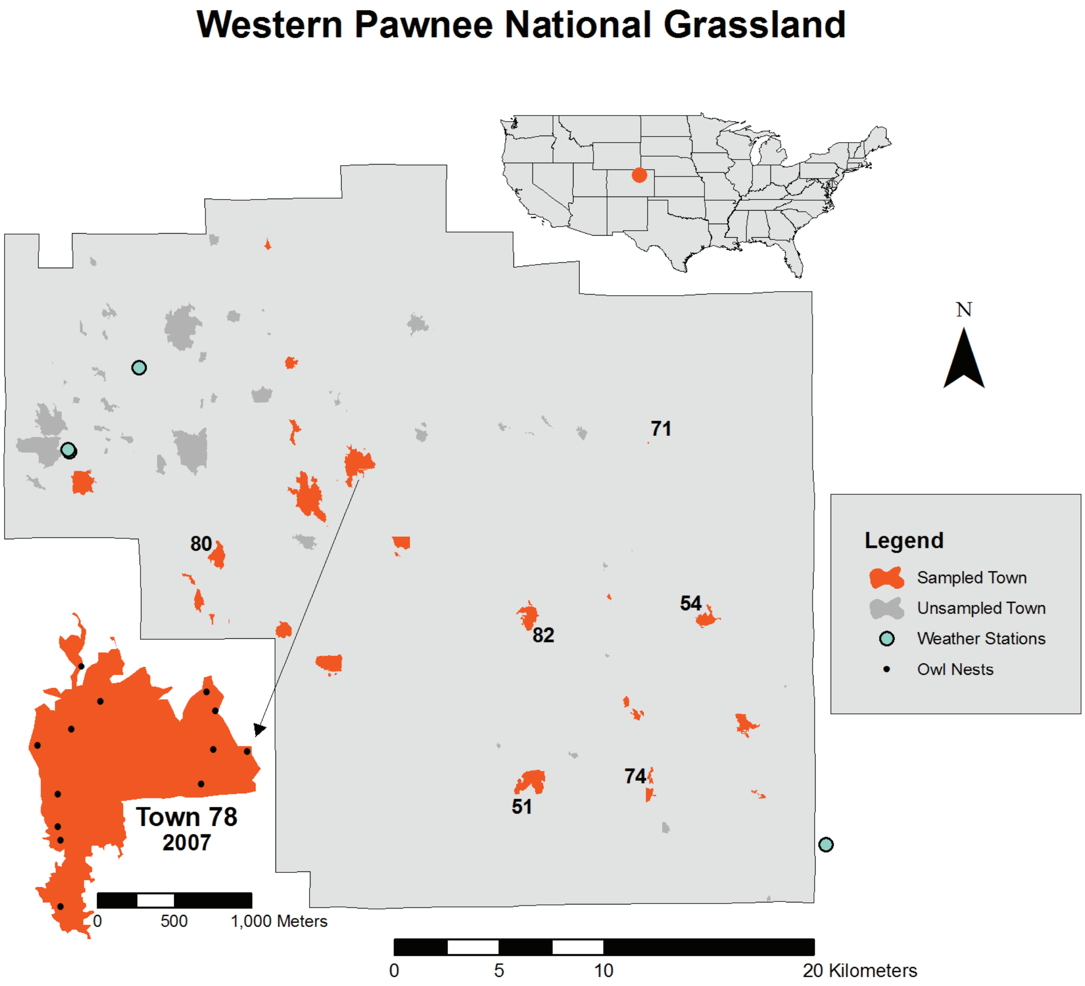

Figure 3.1. Prairie dog towns are displayed at their maximum extent for 2005 – 2008. In any given year, the total area occupied by prairie dog towns was approximately half the displayed area because of colonizations, extinctions, and other fluctuations in town size. Labeled towns were the focus of pellet analyses.

Nest Searches

We searched for adult owls on prairie dog towns and then looked for nest burrows in the vicinity of owl sightings. Early in the nesting season, adult males, who are not involved in incubation or brooding, typically perch conspicuously near the nest burrow during the day. Nest burrows were identified by the presence of shredded mammal manure (Levey et al. 2004), owl feathers, regurgitated pellets, and prey remains such as grasshopper legs, rodent tails, and passerine feathers. A burrow was identified as the site of a nest attempt only if shredded manure, typically cow, prairie dog, or canid, was present ("nest lining": Garcia and Conway 2009). Perching owls, whitewash (mutes), pellets, and prey remains were often seen at perch locations near a nest, but in our experience, shredded manure was present only at nests. We conducted a minimum of three complete surveys on each prairie dog town so that a removal method (Hayne 1949; Otis et al. 1978; White et al. 1982; Rosenberg and Haley 2004) could be used to estimate nest abundance and probability of nest detection.

Monitoring Reproduction

Visual counts of the area surrounding each owl nest using spotting scopes produced an estimate of the minimum number of owlets known alive. We counted owlets for ≥ 15 min. at all nests and recorded the maximum number of owlets at each nest every 5 min. If we were unsure where an owlet belonged, we observed it until it moved to a nest, joined other owlets, or was fed by an adult. In the few cases (under five per year) where the nest could not be identified, the owlet was not counted. Each owlet was aged according to behavior, plumage characteristics, and size (Priest 1997). For analysis, owlets that could not be aged because our view was blocked or too brief were assigned the mean age for that nest. Presence of adults was noted, because lack of adult activity may indicate nest failure, as do prairie dogs in the burrow or cobwebs covering the entrance.

Nests were monitored once per week whenever possible, but the longest interval between observations was 13 days. We monitored each nest until all owlets at that nest were considered to be older than 50 days (d). Fledging of owlets at each nest may be staggered across a week or more, because females lay one egg every 1 – 2 days and usually begin incubation with the first egg (Bent 1938; Olenick 1990; Haug et al. 1993). Following Haug (1985) and Desmond and Savidge (1999), we used 42 d as fledging age, within the range of 35 – 44 d used by others (Thomsen 1971; Landry 1979; Todd et al. 2003; Davies and Restani 2006; Lantz and Conway 2009). Burrowing owl fledglings fly fairly well and are somewhat independent, as parental care such as feeding generally becomes less frequent after this age.

Logistics required that we consider an owlet to be fledged if observed at ≥ 35 d, because when nests are monitored once per week, owlets that have actually reached fledging age of 42 d are more likely to leave the nest area and remain undetected. Owlets within nests do not simultaneously reach 35 d, so while it would be ideal to count an owlet as fledged only if that particular individual was ≥ 35 d old, we could not age all owlets during each observation and considered all owlets as fledging at once from a particular nest with average age ≥ 35 d. Successful nests had at least one owlet known alive when average owlet age was ≥ 35 d. Fledging success per nest was equal to the largest number of owlets ever observed when average owlet age was ≥ 35 d.

Sample Collection

We collected regurgitated pellets and prey remains at least twice during each 2005 – 2007 breeding season from nests, perches, and satellite burrows: once when the nest was discovered in May – early June, and again in July prior to fledging of most nests. Additional collections were made opportunistically, but nest visits were kept to a minimum to avoid disturbing owls. We collected every pellet, rodent tail, foot, bird wing, crayfish claw or similar item, two or more of every feather type, and a sample of more numerous items such as grasshopper legs and beetle parts. Any prey item with consumable parts remaining was left on the ground, and a digital photo was taken instead. A few authors have reported that pellets containing invertebrate prey may disintegrate faster than those containing vertebrates (Marti 1974; York et al. 2002), so we did our best to sample evenly by including pellets that were beginning to separate into pieces. Pellets, insect parts, and feathers were stored at room temperature in sealed paper envelopes, while any prey items with fleshy parts were frozen in ziplock bags.

We subsampled our pellet collection, focusing on six prairie dog towns (Fig. 3.1) with varying plague histories and owl nest densities. These towns were randomly chosen from a stratified set of those with adequate sample size, except that town 71 was chosen as the only long inactive prairie dog town ever to contain an owl nest. A smaller number of additional pellets was analyzed from other towns. We analyzed all prey remains, but time constraints required that we sample our pellet collection by randomly selecting three (if mostly intact) to four (if at least one was broken) pellets per location per sampling date. We sampled all nests from those towns in 2005 and 2007, but in 2006 when the total number of nests was much larger, we randomly selected a subset of nests for diet analysis. For the three towns where we had collections before and after plague epizootics, we analyzed $n+1$ nests in 2006, where n was the number of nests on that town in either 2005 (towns 80 and 82) or 2007 (town 74). Pellets were measured by length and diameter and categorized as loose, broken, mostly intact, or intact.

Prey Identification and Quantification

An overnight soak in 8% (2 molar) NaOH (Degn 1978) was needed to dissolve keratin-based materials such as clumped hair and feather dust that obscured small bones and insect chitin. Prior to soaking, we removed digestible materials that would be useful for identification, such as intact fur, feathers, or claws. Following an overnight soak, we used small round-bottomed metal strainers to rinse samples in tap water prior to placing the strainers in oven-proof bowls for drying at 50°C.

Prey items were identified with the aid of a reference collection, field guides, illustrations, and in difficult cases, expert opinion. We assembled a reference collection of skins, skeletons, and whole arthropods from collections owned by the Shortgrass Steppe Long Term Ecological Research project (specimens collected on the PNG), Denver Museum of Nature and Science, Colorado State University's C. P. Gillette Museum of Arthropod Diversity, as well as CSU's Mammalogy and Ornithology collections. An insect guide (Eaton and Kaufman 2007) and several publications that provided drawings of disarticulated bits of prey organisms (Yalden and Morris 1990; Anderson 1993; Shiel et al. 1997) were helpful. Jaws, dentition, femurs, humeri, and overall bone size were used to identify mammals. Feathers and beaks were used to identify birds. Herpetofauna were identified by the appearance of spades on hind feet (toads), vertebrae count (snakes), length of digits (lizards), and other skin/scale characteristics, because skeletons were not available. Heads, jaws, mandibles, pronota, elytra, legs, and ovipositors were used to identify invertebrates.

Counts were conservative; typically one or fewer individual vertebrates were present in a pellet. Without evidence to the contrary, we assumed that bones from the same species, spread across multiple pellets from the same nest and date, came from just one individual prey organism. We counted more than one individual only if we found too many jaws, femurs, etc. or differently aged prey apparent from tooth wear or bone size. Invertebrate counts were also conservative; for example, for each beetle family, a head and pronotum were assumed to come from the same individual. Counts were typically based on heads for beetles and hymenopterans, and on mandibles or ovipositors for orthopterans. Vertebrates were identified to species whenever possible, and invertebrates were identified to family.

Biomass Calculation

Average small mammal weights from PNG captures were provided by Stapp (unpub. data). Bird weights were reported in Birds of North America Online (Poole 2005; App. 1). Amphibian and reptile weights were not available from a central source, so we searched the primary literature for biomass measurements of the most commonly encountered species (App. 1). Several invertebrate weights were taken from the primary literature (App. 1), but most "wet" weights were calculated from dry weights collected on the PNG from 1970 – 1974 (Dickinson unpub. data). We used SYSTAT version 13 (SYSTAT 2009) to regress wet weights for nine invertebrate families and orders from captures on the PNG and nearby Larimer County (Marti 1974) on the corresponding dry weights from the much larger set of PNG invertebrate captures by Dickinson. Based on examination of a plot of these nine data points, we used a quadratic and a linear term with no intercept (because if dry weight is zero, wet weight should also be zero). We used the resulting regression equation ($R^2 = 0.827$, $F = 16.75$, $P = 0.002$) to calculate biomass for invertebrate taxa: $wet = -626.679dry^2 + 39.115dry$.

Precipitation Data

We downloaded daily precipitation values from five weather stations (Fig. 3.1). Four were located on the Central Plains Experimental Range in the northwestern PNG. Three were located together: two (manual Station 11 and automatic Station 12) were administered by the SGS LTER, and one (CO22) was administered by the National Atmospheric Deposition Program. All three were included because one station may have missing data while the others are functioning, and different collection methods may cause variation in measurements. The fourth station on the CPER was administered by the USDA Agricultural Research Service and was located 5 km to the northeast. These four stations were at the northwest corner of our study area. The fifth station was located at Briggsdale at the southeast corner of our study area and was administered by the National Oceanic and Atmospheric Administration. We based our calculations of site-wide average daily precipitation value on the relative locations of these stations. Weights were as follows: Briggsdale (1/2), ARS (1/4), Station 11 (1/12), Station 12 (1/12), and CO22 (1/12). This system gave equal weight to stations at opposite corners of the study region: Briggsdale at one corner, and the other stations at the opposite corner, including Stations 11, 12, and CO22 at the same location.

These weighted precipitation data were positively correlated (Pearson's $r = 0.899$, $t = 35.98$, $df = 309$, $P < 2.2 \times 10^{-16}$) with spatially interpolated PRISM data (PRISM Climate Group, Oregon State University). Breeding season precipitation totals were

10.15 mm higher for our data, on average, compared to PRISM totals. However, we used data from four weather stations on the W PNG (1 km from the nearest prairie dog town) and from one station (Briggsdale) 500 m from the study area boundary (Fig. 3.1). PRISM used only the Briggsdale station, plus a number of more distant weather stations in Weld and surrounding counties. Because the nearest of these was > 19 km from the W PNG boundary and > 27 km from the nearest sampled prairie dog town, our data were probably more accurate, and the small differences between interpolated precipitation values would not have changed our characterization of wet and dry years. Spatial variation in rainfall across the W PNG cannot be accurately estimated until more stations exist with better spatial coverage.

Missing values led to underestimates in precipitation totals, so we filled missing values using average precipitation values for the nearby stations within our dataset; in such a dry area, many of the missing values were likely zeroes. If ≥ 14 days had missing values for a particular station within a given month, then that station was not used for calculation of that month's total precipitation. We used the daily precipitation values to calculate monthly, seasonal, and annual totals.

Prairie Dog Town Data

The Forest Service has mapped prairie dog towns and reported on extinctions, colonizations, and the area occupied by active burrows since 1981. We classified towns based on their past and present prairie dog town dynamics. Number of years since the most recent plague epizootic was 0 (current epizootic), 1, or ≥ 2 years. Mean town size was 36.87 ha (40.37 SD) and ranged from 0.31 – 187.25 ha. Towns were categorized as extinct due to plague (no known prairie dogs), small with rapid growth, or large with slow growth. Small, rapidly growing towns averaged 9.2 ha with high prairie dog activity pushing the town boundary and relatively large year to year changes in area. Large, slowly growing towns averaged 70.8 ha with relatively small year to year changes in area. Owl nest density was categorized as high, medium, or low. High density towns had more nests per area and smaller average distances between nests. Mean nearest neighbor distance was 105.8 m for nests on high density towns, 279.8 m on medium density towns, and 372.8 m on low density towns.

Statistical Analyses

We recorded and analyzed prey from pellets and remains separately. Prey items in pellets were consumed by owls, while items collected as remains were the "leftover" parts not consumed such as tails and feathers. The time scale that we sampled with pellets and remains may be slightly different, because pellets may disintegrate at a different rate than remains decompose, blow away, or are buried, depending on the weather and level of prairie dog digging and scavenger activity. Statistical analyses were performed only on proportions by number, because the amount of biomass consumed was uncertain when tails and feet were discarded and age and size of prey varied. Proportions rather than raw counts were used because of unequal sampling due to asynchronous nest initiation and fledging dates; some nests fledged prior to the second collection, so fewer pellets and remains were found at these nests.

We used multi-response permutation procedures (MRPP: Zimmerman et al. 1985; McCune and Grace 2002) to test for differences in prey species composition among groups of nests with BLOSSOM version W2008.04.02 (Cade and Richards 2005). MRPP is a nonparametric test that does not assume any underlying distribution or homogeneity of variances. Using the standard MRPP option within BLOSSOM, intragroup distances were calculated with a Euclidean distance function and compared to other permutations under the null hypothesis of no difference between groups. The test statistic and *P*-value were approximated from a Pearson type III distribution with parameters for mean, standard deviation, and skewness. We also ran the same tests without commensuration (no data standardization: "NOCOM" option within BLOSSOM). The commensuration procedure was optional with our data because they had already been standardized and placed on the same numerical scale when we converted counts to proportions. However, commensuration sometimes provides more powerful hypothesis tests and is the default and most commonly used option with MRPP (Mielke and Berry 1999, 2001; Cade and Richards 2005).

The response variables were the proportions of prey items at each owl nest. Continuous covariate data cannot be used in MRPP, so nests had to be grouped (e.g., high and low rainfall). We grouped owl nests by year, rainfall, years since plague epizootics, town dynamics, density of owl nests on towns, nest fate, and fledging success. Years were 2005, 2006, or 2007. Rainfall was categorized as high (2005 and 2007) or low (2006). Number of years since the most recent plague epizootic was 0 (current epizootic), 1, or ≥ 2 years. Towns were categorized as extinct due to plague (no known prairie dogs), small with rapid growth, or large with slow growth. Owl nest density on each town was categorized as high, medium, or low. Nests were successful (fledged at least one owlet) or failed. Nests were divided into those fledging at least four owlets and those fledging fewer owlets.

For pellets, prey species were analyzed at four taxonomic levels: vertebrate versus invertebrate, class (bird, mammal, insect), invertebrate family, and vertebrate species. Because only vertebrate prey remains were reliably sampled, vertebrate remains were analyzed at three taxonomic levels: vertebrate class (herpetofauna, bird, mammal), all vertebrate species, and bird species. Birds were analyzed separately because this is the only taxon that could almost always be identified from remains such as feathers but not pellets. Their hollow bones were typically broken in pellets, so beaks were usually required for identification. The 91 nests for which pellets were analyzed were divided into two or three groups for each analysis, so the sample size per group ranged from six nests on extinct towns to 66 nests on towns with 2+ years since plague events. For analyses of prey remains at 270 nests, the sample size per group ranged from 19 nests on extinct towns to 182 nests fledging fewer than four owlets. Because identification of herpetofauna was often possible only to the level of order or family and these classes were less abundant than all others, we grouped amphibians and reptiles for analysis. Except for kangaroo rats, most rodents have small enough tails and legs for owls to consume, so they often appear in pellets rather than being discarded. These species were combined into two groups for analysis of prey remains: the grasshopper mice and ground squirrels that live in dryer, upland sites including prairie dog towns, and all other species that prefer sites with higher cover such as roadsides, shrublands, and wetter sites.

If the MRPP analysis indicated potential differences in prey species composition between groups, then indicator species analysis (ISA: Dufrene and Legendre 1997;

McCune and Grace 2002) was used to determine which prey taxa best identified those groups. The indicator value (IV: sometimes called "importance value") was calculated for each taxon in each group as relative abundance*relative frequency, so a strong indicator had to be both abundant in samples and spread across many samples within a group. Perfect indicators have IV = 1, and non-indicators have IV = 0. The null hypothesis was that an observed maximum IV across groups was no larger than expected by chance. Significance of indicator values was analyzed using a Monte Carlo randomization in which observed maximum IVs for each taxon were compared to those from 1000 trials in which the owl nests were randomly shuffled among groups. We did not use Bonferroni corrections, because pellets and prey remains were different data sets, and each test evaluated a separate hypothesis (Miller 1981; Rice 1989; Cabin and Mitchell 2000); a rejection of the null hypothesis for one taxonomic group and one independent variable did not imply rejection of any global null hypothesis. Use of the sequential Bonferroni procedure (Holm 1979) has been discouraged for complex and multivariate datasets due to the large inflation of Type II error (Saville 1990; Moran 2003), and other authors have not used it for ISA (e.g., Scott et al. 2003; Abella and Covington 2004; Bangert and Slobodchikoff 2006).

ISA was performed in R version 2.8.1 (R Development Core Team 2008) using the Dufrene-Legendre Indicator Species Analysis (*duleg*) function within the labdsv package (Roberts 2007). Owl nests were grouped with the same ecological variables and analyzed at the same four taxonomic levels as in MRPP. We interpreted results of statistical tests by examining IVs and effect sizes (differences in proportions among groups) as well as *P*-values (Yoccoz 1991), and by comparing results between pellets and prey remains and between MRPP and ISA at different taxonomic levels.

RESULTS

Prey Use

We analyzed a subsample of pellets, quantifying 6774 prey items in 501 pellets from 91 nests (out of 296 total nests). The most common classes identified in owl pellets were insects, mammals, birds, and arachnids, in that order (Table 3.1). Insects were the largest taxonomic group by number (95% of prey items), but small mammals were the largest class by biomass (67% of prey biomass: Fig. 3.2). Ground beetles, grasshoppers, scarab beetles, darkling beetles, and ants were the most common insects consumed by owls and are also the most widespread and abundant families on the PNG (Crist 2008). Horned larks were the most common bird, and all but two arachnids identified in owl pellets were windscorpions.

Ord's kangaroo rat and *Perognathus* pocket mice were the most common mammals eaten by burrowing owls, but almost all mammals known to occur on the PNG (Stapp 2007; Stapp et al. 2008) were identified from pellets (App. 2). Although invertebrate use may reflect their relative availability on prairie dog towns and upland prairie, vertebrate use does not: of the commonly consumed vertebrates, only Northern grasshopper mice, 13-lined ground squirrels, and horned larks are common on prairie dog towns (Stapp 1996; Stapp 2007). The other prey species are more common off towns in shrub lands and denser vegetation; many of the mammalian prey occur in the dense vegetation accompanying roadsides and fencerows. Mammal use did reflect overall availability across the larger shortgrass system on the PNG: counts in pellets were correlated (Pearson's r = 0.764, t = 3.56, df = 9, P = 0.003) with counts from trapping records from 1994 – 2008 (Stapp unpub. data). However, use was more even across species than expected; more voles, pocket mice, and pocket gophers were consumed, and fewer ground squirrels were consumed than expected based on their relative abundance.

Table 3.1. Prey Found in Owl Pellets. The most common of 6774 total prey items counted in 501 regurgitated burrowing owl pellets were insects, mammals, birds, and arachnids. While invertebrates dominated prey numbers, vertebrates, especially mammals, dominated prey biomass. Proportions by number of these common prey items were used in statistical analyses of invertebrate families and vertebrate species. For each taxon, we calculated proportion within the class (Pclass) and proportion of total (Ptotal). Non-rodent mammals and non-passerine birds were mainly unknown specimens.

Latin Name	**Common Name**	**Number of Indiv**			**Biomass**
		Count	PClass	PTotal	PTotal
Class Insecta	insects	6412	1.0000	0.9466	0.1132
Order Coleoptera	beetles	4447	0.6935	0.6565	0.0589
Family Carabidae	ground beetles	2369	0.3695	0.3497	0.0273
Family Scarabaeidae	scarab beetles	966	0.1507	0.1426	0.0059
Family Tenebrionidae	darkling beetles	779	0.1215	0.1150	0.0179
Family Silphidae	carrion beetles	103	0.0161	0.0152	0.0042
Family Curculionidae	weevils	83	0.0129	0.0123	0.0007
Family Cerambycidae	long-horned beetles	55	0.0086	0.0081	0.0016
Superfamily Elateroidea	click, firefly, soldier beetles	24	0.0037	0.0035	0.0005
Order Orthoptera	grasshoppers, crickets	1454	0.2268	0.2146	0.0511
Family Acrididae	short-horned grasshoppers	1243	0.1939	0.1835	0.0465
Family Rhaphidophoridae	camel crickets	201	0.0313	0.0297	0.0042
Order Hymenoptera	bees, ants	452	0.0705	0.0667	0.0025
Family Formicidae	ants	407	0.0635	0.0601	0.0022
Order Diptera	flies	25	0.0039	0.0037	0.0001
Class Arachnida	arachnids	22	1.0000	0.0032	0.0005
Order Solifugae	windscorpions	20	0.9091	0.0030	0.0005
Family Eremobatidae	straight-faced windscorpions	20	0.9091	0.0030	0.0005
Class Malacostraca	crabs, lobster, shrimp, pillbugs	3	1.0000	0.0004	0.0003
Order Decapoda	crabs, lobster, shrimp	3	1.0000	0.0004	0.0003
Family Cambaridae	cambarid crayfish	3	1.0000	0.0004	0.0003

Class Mammalia	mammals	243	1.0000	0.0359	0.6655
Order Rodentia	rodents	236	0.9712	0.0348	0.6463
Family Heteromyidae	pocket mice, kangaroo rats	65	0.2675	0.0096	0.1675
Perognathus sp.	small pocket mice	32	0.1317	0.0047	0.0203
Dipodomys ordii	Ord's kangaroo rat	30	0.1235	0.0044	0.1395
Family Muridae	mice and voles	97	0.3992	0.0143	0.1640
Peromyscus maniculatus	deer mouse	22	0.0905	0.0032	0.0315
Reithrodontomys sp.	harvest mice	19	0.0782	0.0028	0.0156
Microtus sp.	voles	19	0.0782	0.0028	0.0449
Onychomys leucogaster	Northern grasshopper mouse	17	0.0700	0.0025	0.0381
Family Sciuridae	squirrels	20	0.0823	0.0030	0.1669
Spermophilus tridecemlineatus	13-lined ground squirrel	19	0.0782	0.0028	0.1586
Class Aves	birds	84	1.0000	0.0124	0.2000
Order Passeriformes	passerines	70	0.8333	0.0103	0.1666
Family Alaudidae	larks	28	0.3333	0.0041	0.0650
Eremophila alpestris	horned lark	28	0.3333	0.0041	0.0650
Class Reptilia	reptiles	6	1.0000	0.0009	0.0173
Order Squamata	lizards and snakes	6	1.0000	0.0009	0.0173
Family Colubridae	colubrid snakes	2	0.3333	0.0003	0.0110
Family Phrynosomatidae	phrynosomatid lizards	3	0.5000	0.0004	0.0033
Class Amphibia	amphibians	4	1.0000	0.0006	0.0032
Order Anura	frogs and toads	4	1.0000	0.0006	0.0032

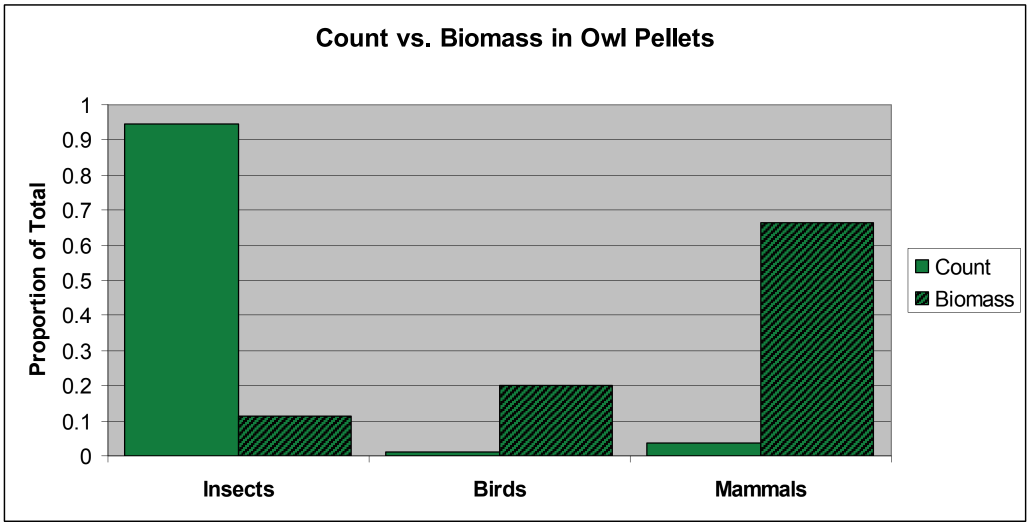

Figure 3.2. Most prey individuals in owl pellets were insects, but their overall biomass (# individuals*biomass per individual) was quite small compared to birds or mammals.

Prey remains were analyzed separately from pellets. We analyzed all 1348 prey remains from 270 nests and their associated perches and satellite burrows over three breeding seasons. Of these, 757 were insect remains, of which 517 were grasshoppers, whose large rear legs were rarely consumed. The most common classes of large prey identified in owl prey remains were birds, mammals, crayfish, reptiles, and amphibians (Table 3.2). The horned lark was the most abundant vertebrate identified from prey remains, and Ord's kangaroo rat was by far the most common mammal. Three species accounted for 90% of avian prey identified from prey remains (mostly feathers and wings): horned larks (*Eremophila alpestris*), lark buntings (*Calamospiza melanocorys*), and McCown's longspurs (*Calcarius mccownii*). Along with western meadowlarks (*Sturnella neglecta*), these species were the most common passerines breeding on the PNG from 2005 – 2008 (USGS Patuxent Wildlife Research Center 2010). Crayfish, reptiles, and amphibians were far less abundant in prey remains. Birds dominated counts of large prey remains (56%), but mammals had higher biomass (51%: Fig. 3.3).

Table 3.2. Large Prey Identified from Owl Prey Remains. The most common of 589 non-insect prey items counted as prey remains at 270 nests were birds, mammals, crayfish, reptiles, and amphibians. While birds dominated prey numbers, mammals dominated prey biomass. Proportions by number of vertebrates only were used in statistical analyses; other than crayfish, invertebrates were too small and numerous to collect each piece. For each taxon, we calculated proportion within the class (Pclass) and proportion of total (Ptotal). Burrowing owl feathers and prairie dog remains were not included in analyses, because their presence at nests and perches was probably not indicative of predation by owls.

Latin Name	**Common Name**	**Number of Indiv**			**Biomass**
		Count	PClass	PTotal	PTotal
Class Aves	birds	328	1.0000	0.5569	0.4246
Order Passeriformes	passerines	314	0.9573	0.5331	0.4065
Family Alaudidae	larks	168	0.5122	0.2852	0.2120
Eremophila alpestris	horned lark	168	0.5122	0.2852	0.2120
Family Emberizidae	sparrows and allies	127	0.3872	0.2156	0.1699
Calamospiza melanocorys	lark bunting	85	0.2591	0.1443	0.1255
Calcarius mccownii	McCown's longspur	34	0.1037	0.0577	0.0337
Class Mammalia	mammals	196	1.0000	0.3328	0.5141
Order Rodentia	rodents	187	0.9541	0.3175	0.4905
Family Heteromyidae	pocket and kangaroo mice	143	0.7296	0.2428	0.3617
Dipodomys ordii	Ord's kangaroo rat	142	0.7245	0.2411	0.3591
Family Muridae	mice and voles	18	0.0918	0.0306	0.0228
Microtus sp.	voles	11	0.0561	0.0187	0.0141
Onychomys leucogaster	northern grasshopper mouse	4	0.0204	0.0068	0.0049
Family Sciuridae	squirrels	15	0.0765	0.0255	0.0681
Spermophilus tridecemlineatus	13-lined ground squirrel	15	0.0765	0.0255	0.0681
Family Geomyidae	pocket gophers	8	0.0408	0.0136	0.0300
Thomomys talpoides	N. pocket gopher	8	0.0408	0.0136	0.0300
Class Malacostraca	crabs, lobster, shrimp, pillbugs	27	1.0000	0.0458	0.0016
Order Decapoda	crabs, lobster, shrimp	27	1.0000	0.0458	0.0016
Family Cambaridae	cambarid crayfish	27	1.0000	0.0458	0.0016

Class Reptilia	reptiles	24	1.0000	0.0407	0.0497
Order Squamata	lizards and snakes	23	0.9583	0.0390	0.0476
Family Colubridae	colubrid snakes	11	0.4583	0.0187	0.0330
Family Phrynosomatidae	phrynosomatid lizards	7	0.2917	0.0119	0.0042
Phrynosoma hernandesi	short-horned lizard	5	0.2083	0.0085	0.0030
Class Amphibia	amphibians	14	1.0000	0.0238	0.0101
Order Anura	frogs and toads	10	0.7143	0.0170	0.0044
Family Pelobatidae	spadefoot toads	5	0.3571	0.0085	0.0022
Spea bombifrons	plains spadefoot toad	5	0.3571	0.0085	0.0022
Order Caudata	salamanders	4	0.2857	0.0068	0.0057
Family Ambystomatidae	mole salamanders	4	0.2857	0.0068	0.0057
Ambystoma tigrinum	tiger salamander	4	0.2857	0.0068	0.0057

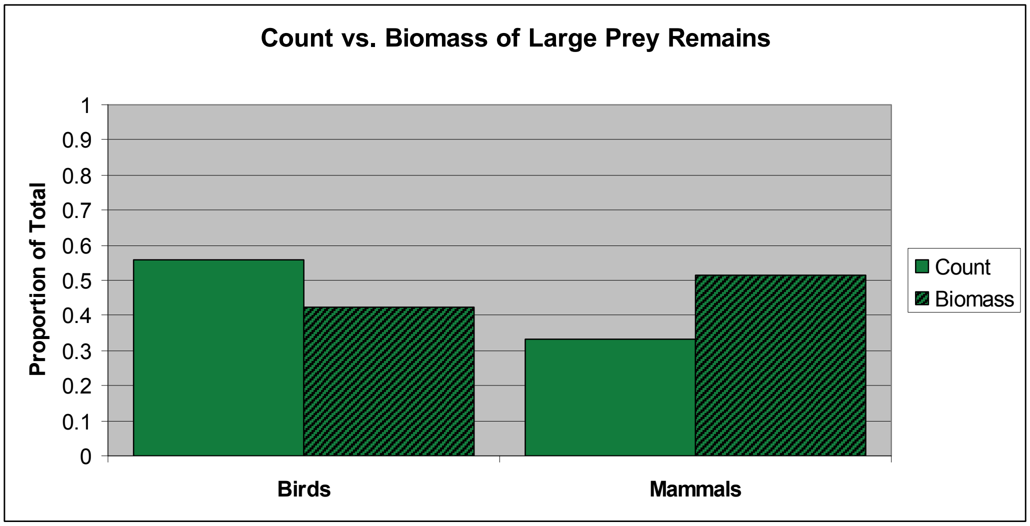

Figure 3.3. Although birds dominated numbers of individuals identified from large prey remains (vertebrates and crayfish), mammals were more important prey items when biomass (# individuals*biomass per individual) was considered.

MRPP

MRPP analysis of prey composition of owl pellets revealed significant differences ($p < 0.1$) associated with year, rainfall, nest success, and fledging success, marginal differences related to owl nest density, and no effect due to plague (Table 3.3). Differences in composition occurred mainly for classes and vertebrate species. Results from MRPP analyses were similar whether or not commensuration was used.

Table 3.3. MRPP Differences in Composition of Owl Pellets. Multi-response permutation procedures revealed differences in the species composition of burrowing owl pellets associated with year, rainfall, nest success, and fledging success. Owl nest density was associated with marginal differences in composition, and plague had no effect. Most of the differences in prey composition occurred at the level of class or vertebrate species. Sample units were owl nests, and commensuration was used in these analyses. Bold font indicates $p < 0.1$.

Variable	Taxa Level	Test Stat	p-value
Year	VertInvert	-1.286	0.105
Year	**Class**	-1.812	0.058
Year	InvertFam	-1.116	0.133
Year	**VertSpp**	-1.346	0.097
Rain	VertInvert	-0.857	0.150
Rain	Class	-1.279	0.103
Rain	**InvertFam**	-2.082	0.038
Rain	VertSpp	-1.159	0.126
PlagueYr	VertInvert	0.126	0.445
PlagueYr	Class	-0.039	0.392
PlagueYr	InvertFam	-1.121	0.132
PlagueYr	VertSpp	-0.162	0.390
TownDyn	VertInvert	-0.612	0.214
TownDyn	Class	0.434	0.596
TownDyn	InvertFam	0.849	0.798
TownDyn	VertSpp	-0.256	0.353
Density	VertInvert	-1.166	0.119
Density	Class	-1.225	0.113
Density	InvertFam	-0.305	0.337
Density	VertSpp	1.179	0.896
NestSucc	VertInvert	0.976	1.000
NestSucc	**Class**	-1.466	0.085
NestSucc	InvertFam	1.652	0.996
NestSucc	**VertSpp**	-1.702	0.061
Fledge 4	VertInvert	-0.968	0.135
Fledge 4	**Class**	-1.533	0.079
Fledge 4	InvertFam	0.648	0.712
Fledge 4	VertSpp	-0.699	0.220

Years were 2005, 2006, or 2007. Rainfall was categorized as high (2005 and 2007) or low (2006). Number of years since the most recent plague epizootic was 0 (current epizootic), 1, or ≥ 2 years. Towns were categorized as extinct due to plague, small with rapid growth, or large with slow growth. Owl nest density was categorized as high, medium, or low. Nests were successful (fledged at least one owlet) or failed. Nests were divided into those fledging at least four owlets and those fledging fewer owlets. Prey were analyzed at four taxonomic levels: vertebrate versus invertebrate, class (birds, mammals, insects), invertebrate family, and vertebrate species.

MRPP analysis of composition of owl prey remains (vertebrates) revealed significant differences ($p < 0.1$, most $p < 0.05$) associated with year, rainfall, time since plague, owl nest density, and fledging success, and no effect related to prairie dog town dynamics or nest success (Table 3.4). Compositional differences existed at all taxonomic levels. Results from prey remains largely corresponded to those for owl pellets. Differences were likely related to the deposition rate and longevity of prey remains on the ground versus pellets, the larger sample size for analysis of prey remains (three times more nests), and our ability to separate bird species with feather remains but not with bone fragments in pellets.

Table 3.4. MRPP Differences in Composition of Owl Prey Remains. Multi-response permutation procedures revealed differences in the species composition of burrowing owl prey remains (unconsumed prey parts) associated with year, rainfall, time since plague, owl nest density, and fledging success. Prairie dog town dynamics and nest success were unrelated to owl diet. Sample units were owl nests, and commensuration was used in these analyses. Bold font indicates $p < 0.1$.

Variable	Taxa Level	Test Stat	p-value
Year	**Class**	-8.275	0.000
Year	**VertSpp**	-7.083	0.000
Year	**BirdSpp**	-5.168	0.000
Rain	**Class**	-5.499	0.001
Rain	**VertSpp**	-4.654	0.001
Rain	**BirdSpp**	-3.816	0.006
PlagueYr	**Class**	-1.988	0.046
PlagueYr	VertSpp	-0.666	0.226
PlagueYr	**BirdSpp**	-2.649	0.019
TownDyn	Class	-0.410	0.278
TownDyn	VertSpp	0.218	0.528
TownDyn	BirdSpp	-0.417	0.283
Density	Class	-0.544	0.243
Density	**VertSpp**	-4.895	0.000
Density	**BirdSpp**	-1.415	0.091
NestSucc	Class	0.764	0.776
NestSucc	VertSpp	0.359	0.575
NestSucc	BirdSpp	0.564	0.657
Fledge 4	**Class**	-2.166	0.041
Fledge 4	VertSpp	-1.209	0.117
Fledge 4	BirdSpp	0.741	0.756

Years were 2005, 2006, or 2007. Rainfall was categorized as high (2005 and 2007) or low (2006). Number of years since the most recent plague epizootic was 0 (current epizootic), 1, or ≥ 2 years. Towns were categorized as extinct due to plague, small with rapid growth, or large with slow growth. Owl nest density was categorized as high, medium, or low. Nests were successful (fledged at least one owlet) or failed. Nests were divided into those fledging at least four owlets and those fledging fewer owlets. Prey were analyzed at three taxonomic levels: class (herpetofauna, birds, mammals), vertebrate species, and bird species.

Indicator Species

Indicator species analysis identified specific prey associations (Tables 3.5 – 3.6) for the ecological variables we tested after compositional differences were suggested by MRPP. Several vertebrates were associated with specific years. Insects and several rodents were indicators for dry weather, while birds in particular were associated with wet summers. Bird consumption was associated with nest failure and mammal consumption with nest success and high productivity. There was some indication that fewer vertebrates were consumed where nest density was high. There were no indicator taxa for plague year. The largest indicator values (IV > 0.4) with the largest inter-group differences occurred for birds in wet summers and at failed nests.

Table 3.5. Indicator Taxa from Owl Pellets. Indicator species analysis was used to determine which prey taxa from owl pellets best identified groups of owl nests. Perfect indicators have IV = 1, and non-indicators have IV = 0. Indicator values were calculated whenever multi-response permutation procedures (MRPP) suggested that differences existed in prey species composition among groups.

(a) Northern grasshopper mice were associated with 2006 and horned larks with 2007. Pocket mice, grasshopper mice, weevils, and grasshoppers were indicators for dryer weather, while flies and birds (particularly horned larks) were indicators for wetter weather.
(b) Insect use was linked with moderate nest density. Birds, particularly horned larks, were associated with failed nests and mammals with successful nests. Kangaroo rats were indicators of productive nests.

(a)	**Year**				**Rain**		
	Indicator Value			p-value	Indicator Value		p-value
	2005	2006	2007		Wet	Dry	
Aves	0.2084	0.0559	0.2353	0.500	**0.4033**	0.0983	0.039
Insecta	0.3205	0.3410	0.3384	0.220	0.4917	0.5083	0.148
Mammalia	0.3665	0.2801	0.1748	0.160	0.4045	0.4294	0.797
Herp	0.0074	0.0529	0.0289	0.687	0.0238	0.0751	0.359
E. alpestris	0.0443	0.0054	**0.2297**	0.008	**0.2263**	0.0101	0.014
Passeriformes	0.0492	0.1117	0.1237	0.743	0.1246	0.1641	0.656
D. ordii	0.0398	0.0998	0.0592	0.725	0.0755	0.1439	0.399
Perognathus	0.0511	0.1398	0.0028	0.128	0.0235	**0.1769**	0.041
Microtus	0.1138	0.1074	0.0000	0.335	0.0381	0.1549	0.132
O. leucogaster	0.0102	**0.1761**	0.0023	0.012	0.0072	**0.2119**	0.003
P. maniculatus	0.0761	0.0746	0.0036	0.601	0.0387	0.1073	0.308
Reithrodontomys	0.0661	0.0468	0.0514	0.936	0.0905	0.0722	0.838
S. tridecemlineatus	0.0351	0.0943	0.0177	0.409	0.0352	0.1304	0.208
Carabidae					0.4136	0.4739	0.502
Cerambycidae					0.1213	0.1195	0.960
Curculionidae					0.0552	**0.2147**	0.080
Elateroidea					0.0731	0.0450	0.707
Scarabaeidae					0.4570	0.3364	0.356
Silphidae					0.2787	0.1342	0.464
Tenebrionidae					0.4431	0.4293	0.881
Diptera					**0.2225**	0.0060	0.023
Eremobatidae					0.0564	0.1040	0.558
Formicidae					0.3277	0.1231	0.162
Hymenoptera					0.0499	0.1221	0.414
Acrididae					0.3769	**0.5774**	0.031
Rhaphidophoridae					0.1126	0.1032	0.926

(b)	**Density**				**NestSucc**			**Fledge 4**		
	Indicator Value			p-	Indicator Value		p-	Indicator Value		p-
	Low	Med	High	value	0	1	value	0	1	value
Aves	0.2806	0.1039	0.0895	0.263	**0.4570**	0.1088	0.018	0.3479	0.1313	0.207
Insecta	0.3197	**0.3447**	0.3357	0.055	0.4965	0.5035	0.598	0.4971	0.5029	0.653
Mammalia	0.2967	0.1862	0.3602	0.263	0.2510	**0.5484**	0.037	0.3560	0.5049	0.149
Herp					0.0723	0.0239	0.432	0.0407	0.0504	0.869
E. alpestris					**0.3111**	0.0171	0.001	0.1328	0.0492	0.411
Passeriformes					0.1574	0.1227	0.767	0.1740	0.1079	0.559
D. ordii					0.0330	0.1731	0.196	0.0382	**0.2652**	0.014
Perognathus					0.0117	0.1583	0.132	0.0285	0.1604	0.129
Microtus					0.1287	0.0540	0.338	0.0476	0.1509	0.205
O. leucogaster					0.0119	0.1314	0.137	0.0414	0.1169	0.264
P. maniculatus					0.0401	0.0874	0.587	0.0670	0.0652	0.948
Reithrodontomys					0.0515	0.1094	0.543	0.0646	0.1022	0.652
S. tridecemlineatus					0.0345	0.1057	0.448	0.0527	0.1088	0.426

Prey were analyzed at three taxonomic levels: class (birds, mammals, insects), vertebrate species, and invertebrate family. Herpetofauna were grouped for analysis, as were passerines except horned larks.

(a) Years were 2005, 2006, or 2007. Rainfall was categorized as high (2005 and 2007) or low (2006).
(b) Owl nest density was categorized as high, medium, or low. Nests were successful (fledged at least one owlet) or failed. Nests were divided into those fledging at least four owlets and those fledging fewer owlets.

Table 3.6. Indicator Taxa from Owl Prey Remains. Indicator species analysis was used to determine which vertebrate prey taxa from owl prey remains best identified groups of owl nests. Perfect indicators have IV = 1, and non-indicators have IV = 0. Indicator values were calculated whenever multi-response permutation procedures (MRPP) suggested that differences existed in prey species composition among groups.

(a) Mammal remains, especially kangaroo rats, were indicators for 2005, while mammals of dense vegetation were indicators for 2006 when weather was dry. Herpetofauna (reptile) and bird (lark bunting) remains were associated with 2007. Bird (lark bunting and horned lark) remains were indicators of wet weather. There were no indicator taxa for plague year.
(b) Lark bunting and rodent remains were linked with low nest density, except that kangaroo rat remains were linked with high density. There were no indicator taxa for nest success. Mammal remains (kangaroo rats and rodents of dense vegetation) were associated with highly productive nests.

(a)	**Year**				**Rain**			**PlagueYr**			
	Indicator Value			p-value	Indicator Value		p-value	Indicator Value			p-value
	2005	2006	2007		Wet	Dry		0	1	2	
Herp	0.0000	0.0389	**0.1227**	0.007	0.0653	0.0513	0.741	0.0143	0.0532	0.0379	0.749
Aves	0.2785	0.1529	**0.3092**	0.031	**0.4716**	0.2421	0.001	0.1142	0.2972	0.2760	0.143
Mammalia	**0.1972**	0.1376	0.0433	0.020	0.1324	0.2102	0.172	0.1320	0.0493	0.1417	0.555
Amphibia	0.0000	0.0281	0.0324	0.451	0.0166	0.0357	0.440	0.0000	0.0487	0.0164	0.194
Reptilia	0.0000	0.0192	**0.0927**	0.010	0.0506	0.0259	0.500	0.0193	0.0184	0.0247	1.000
C. melanocorys	0.0163	0.0487	**0.2194**	0.001	**0.1739**	0.0714	0.093	0.0018	0.1418	0.1207	0.147
C. mccownii	0.0636	0.0220	0.0370	0.359	0.0754	0.0361	0.388	0.0322	0.0695	0.0252	0.340
E. alpestris	0.2262	0.0907	0.2116	0.132	**0.3571**	0.1488	0.005	0.0903	0.1893	0.2021	0.522
D. ordii	**0.1519**	0.0938	0.0438	0.061	0.1193	0.1474	0.584	0.0914	0.0500	0.1106	0.675
Dense rodent	0.0000	**0.1015**	0.0004	0.000	0.0002	**0.1030**	0.000	0.0549	0.0009	0.0099	0.118
Upland rodent	0.0156	0.0278	0.0029	0.555	0.0109	0.0424	0.199	0.0115	0.0015	0.0262	0.687
C. melanocorys	0.0174	0.0540	**0.2047**	0.001	0.1638	0.0784	0.163	0.0015	0.1333	0.1329	0.202
C. mccownii	0.0669	0.0229	0.0330	0.286	0.0730	0.0377	0.441	0.0307	0.0685	0.0275	0.357
E. alpestris	0.2133	0.0993	0.2124	0.252	**0.3415**	0.1591	0.012	0.0980	0.1759	0.2044	0.456

(b)	**Density**				**NestSucc**			**Fledge 4**		
	Indicator Value			p-	Indicator Value		p-	Indicator Value		p-
	Low	Med	High	value	0	1	value	0	1	value
Herp								0.0588	0.0619	0.937
Aves								0.3816	0.3509	0.572
Mammalia								0.1116	**0.2790**	0.005
Amphibia	0.0219	0.0196	0.0074	0.856	0.0176	0.0313	0.672	0.0340	0.0138	0.557
Reptilia	0.0604	0.0117	0.0183	0.139	0.0423	0.0378	0.880	0.0297	0.0563	0.415
C. melanocorys	**0.1387**	0.0870	0.0330	0.090	0.1621	0.1047	0.266	0.1468	0.1039	0.511
C. mccownii	0.0177	0.0397	0.0634	0.361	0.0510	0.0661	0.734	0.0425	0.0857	0.275
E. alpestris	0.1963	0.1179	0.2121	0.274	0.3045	0.2279	0.206	0.2931	0.2169	0.333
D. ordii	0.0333	0.0937	**0.1609**	0.031	0.1027	0.1597	0.406	0.0841	**0.2265**	0.011
Dense rodent	**0.0542**	0.0093	0.0013	0.052	0.0055	0.0426	0.239	0.0069	**0.0572**	0.061
Upland rodent	**0.1134**	0.0012	0.0000	0.000	0.0327	0.0173	0.533	0.0432	0.0051	0.254
C. melanocorys	0.1337	0.0918	0.0326	0.112						
C. mccownii	0.0167	0.0374	0.0688	0.247						
E. alpestris	0.1852	0.1168	0.2257	0.122						

Prey were analyzed at three taxonomic levels: class (herpetofauna, birds, mammals), all vertebrate species, and bird species. Amphibians were grouped for analysis, as were reptiles and mammals except kangaroo rats. Grasshopper mice and ground squirrels are common in dry upland sites and prairie dog towns, while voles, gophers, pocket, deer, and harvest mice are usually associated with denser vegetation.

(a) Years were 2005, 2006, or 2007. Rainfall was categorized as high (2005 and 2007) or low (2006). Number of years since the most recent plague epizootic was 0 (current epizootic), 1, or ≥ 2 years.
(b) Owl nest density was categorized as high, medium, or low. Nests were successful (fledged at least one owlet) or failed. Nests were divided into those fledging at least four owlets and those fledging fewer owlets.

Summary and Effect Sizes

Overall, the largest differences in prey composition were associated with year (one dry versus two wet summers) and the success and productivity of nests for classes and vertebrate species (Tables 3.3 – 3.7; Fig. 3.4). During the driest year of our study, 35% of insects consumed were grasshoppers, compared to 24% in wetter years. No amphibian or reptile remains were collected in 2005, but their use by owls increased through 2007. Mammal use in 2007 was half the 2005 level. While kangaroo rat numbers in pellets doubled after 2005, their presence as prey remains showed the opposite trend. Vole use declined to zero in 2007. Consumption of pocket and grasshopper mice decreased by an order of magnitude from dry 2006 to wetter 2007, with intermediate values in 2005. Remains of rodents of dense vegetation were nearly absent at owl nests in 2005 and 2007, with their proportion in owl diets increasing by > 20 times in the driest year of 2006. The rarity of birds in owl diets during 2006 seemed driven mainly by horned larks; the proportion of horned larks in the diet was 5 – 10 times higher in wetter years with lower nest and fledging success. In contrast, lark bunting use increased each year and tripled from 2005 – 2007.

Table 3.7. Factors Correlated with Prey Use. Year, rainfall, nest fate, and fledging success were significant covariates in MRPP analyses of prey species composition from owl pellets. Results from indicator species analysis and from analysis of prey remains generally confirmed the importance of these relationships. Due to time constraints, diet samples from 2008 were not analyzed, but overall reproductive estimates would appear low without the context of a second dry year. Apparent nest success and fledging success were estimated for 322 nest attempts.

Year	Summer Rainfall (mm)	Nest Success	Fledging Success (juvs/nest)
2005	168	59.4%	1.88
2006	97	79.5%	3.16
2007	150	60.0%	1.88
2008	80	84.6%	3.77
Overall	124	68.6%	2.48

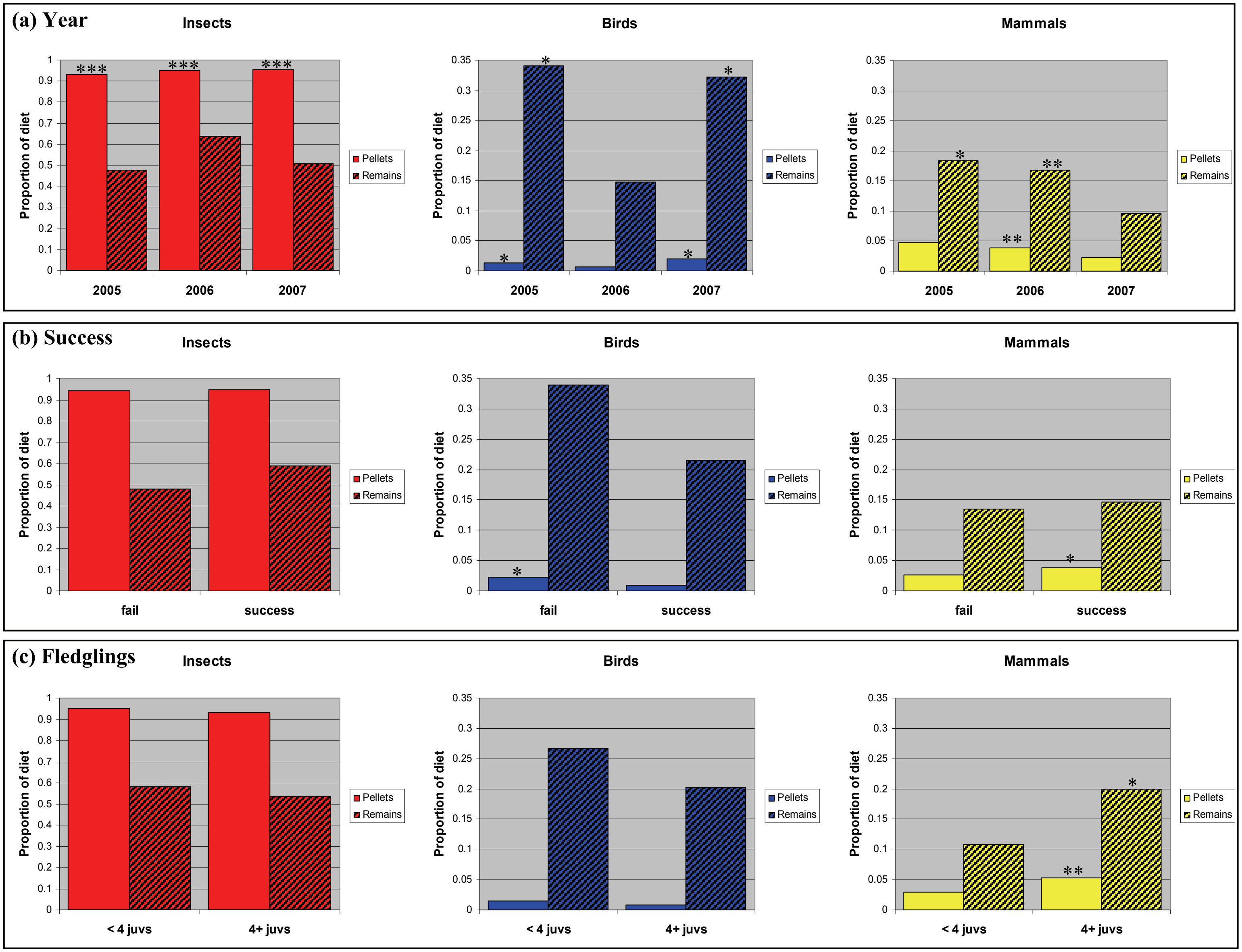
(a) Year
Insects
Birds
Mammals
Proportion of diet
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0.05
0.15
0.25
0.35
***
*
**
2005
2006
2007
Pellets
Remains
(b) Success
Insects
Birds
Mammals
fail
success
(c) Fledglings
Insects
Birds
Mammals
< 4 juvs
4+ juvs

Figure 3.4. Proportion of insect, avian, and mammalian prey items in owl pellets and prey remains differed with year, nest success, and fledging success. The y-axis for insects is higher because insects were a much larger class by number than vertebrates. The sum over each category (e.g., 2005 nests) is slightly < 1 because rarer classes (arachnids, crayfish, reptiles, and amphibians) were not plotted.
* = indicator class, ** = genus in class is an indicator taxon, *** = insect family is an indicator taxon (from Indicator Species Analysis, Tables 3.5 – 3.6)

(a) Insect use did not vary much with year, although more remains, mainly grasshopper legs, were collected in 2006. Some insect families were more common in wet years, and others (mainly grasshoppers) in dry years. Birds were more commonly consumed in wet years (2005 and 2007). As a class, mammals were used most in 2005, but specific genera were consumed most in 2006 (a drought year).
(b) Insect use was not significantly different at failed and successful nests. Bird consumption was associated with failed nests and mammal consumption with successful nests. Nests were successful (fledged at least one owlet) or failed.
(c) Only mammalian prey items were linked to productivity. Nests were divided into those fledging at least four owlets and those fledging fewer owlets.

Vertebrate consumption, as quantified by prey remains but not pellets, decreased with increasing nest density for lark buntings and all rodents except kangaroo rats (Table 3.6b). These species were 20% more common at owl nests in low density towns, while kangaroo rats were 14% more common at nests in high density towns.

Owls at successful and highly productive nests ate fewer birds and more mammals (Tables 3.4 – 3.6; Fig. 3.4). Pellets at successful nests contained half the birds, and a 5-fold decline in horned larks, but 1/3 more mammals than those at failed nests, although proportions by count for both were small compared to insects. Highly productive nests had 10% more mammal remains than less productive nests, and kangaroo rats were the most important indicator of productivity.

We found no indicator taxa related to plague year (Tables 3.5 – 3.6). However, MRPP suggested differences related to avian prey remains (Table 3.4). Horned lark remains increased steadily as time since plague and prairie dog occupancy within towns increased, from 33% to 44% of remains at the average nest. Lark bunting remains were an order of magnitude proportionally less common on extinct towns: 2% on extinct versus 20% on active towns. Longspur consumption showed no trend.

DISCUSSION

Prey Use

Burrowing owls are known to be generalist predators, and our sample of pellets and prey remains contained at least one of almost every known potential prey item on the PNG (App. 2). Based on previous studies, we expected that many insects would be consumed with lower proportional contribution to biomass, but the magnitude of the difference was unexpected: 95% of prey items in pellets were insects (Table 3.1), but insects comprised only 11% of prey biomass (Fig. 3.2). Based on the sizes of fragments found in our samples, many of the ground beetles consumed were very small (2 - 3 mm long), although large *Pasimachus elongatus* were also frequently eaten. Aside from Orthoptera, the only other insect order that was frequently consumed was Hymenoptera, especially ants. Other authors hypothesized that ants (Longhurst 1942; Grimm et al. 1985) and other small arthropods (Schlatter et al. 1980) were incidentally consumed while crawling on larger prey items, because their tiny size should not warrant a concerted effort at foraging for them. However, the high numbers of ants and small beetles we observed in our prey samples suggest that juveniles, who are unable to easily catch vertebrate prey, and adults without other tasks to occupy them at midday, may be targeting ants and other small insects found near the nest that are easy to catch.

Compared to insects, mammals were rare in terms of number (Table 3.1), but they were the most important taxonomic group in terms of biomass (67%: Fig. 3.2). Ord's kangaroo rats and the smaller *Perognathus* pocket mice were most important, but almost every small mammal known to occur on the PNG was consumed. Although invertebrate use may reflect their relative availability on prairie dog towns and upland prairie, vertebrate use did not: of the commonly consumed vertebrates, only Northern grasshopper mice, 13-lined ground squirrels, and horned larks are common in these habitats (Stapp 1996; Stapp 2007). The other prey species are more common off towns in shrublands and denser vegetation; many of the mammalian prey occur in the dense vegetation accompanying roadsides and fencerows (Stapp and Lindquist 2007). This suggests that burrowing owls commonly forage for vertebrates off prairie dog towns, especially at roadsides and fencerows where perches are available and used by other owls and raptors (Marti 1974; Zimmerman et al. 1996). These foraging preferences may provide one explanation for the pattern observed by Orth and Kennedy (2001), in which owls seemed to prefer more fragmented landscapes, particularly given that owls in this and other studies (Toombs 1997; Ekstein 1999; Griebel 2000; Teaschner 2005) often nested near the edges of prairie dog towns (Fig. 3.1). Owls may also select prey based on their size and factors that make them more or less vulnerable to predation.

Horned larks, lark buntings, and McCown's longspurs were common prey items (Table 3.2; App. 2), but other bird species were not. The only species of concern found in diet samples (five individuals) was the mountain plover (*Charadrius montanus*). More were certainly consumed beyond those that we sampled, but it seems unlikely that owl predation is playing a large role in recent plover population declines. Other taxa were consumed at much lower frequency (Tables 3.1 – 3.2; App. 2), but were important for some pairs. Crayfish were uncommon across most of the normally dry PNG, but were often used by several pairs that lived near a water source. A variety of snakes and lizards were predated, including some rather large individuals. We did not find evidence of rattlesnake consumption. Owls did not make much use of amphibians, and many that we sampled were the largely unconsumed dried husks of spadefoot toads, suggesting that owls may find them unpalatable (Schlatter et al. 1980; Green et al. 1993).

We examined long term trends and year to year variation in burrowing owl diet by comparing our results to those in the same area from 1967 – 1969 (Marti 1974) and 2000 (Woodard 2002). Long term steep declines in the consumption of deer mice and voles were apparent in both this study and Woodard (2002), compared to the high frequency of these prey species in Marti (1974). We found 1/9 the *Microtus* and 1/12 the *Peromyscus* that Marti (1974) counted in owl pellets. For many prey taxa, a comparison of these three studies suggests that either long term changes or year to year variation may be occurring, because proportions in our study were quite different from either of the earlier studies. We found higher frequencies of darkling beetles (2 – 6 times higher), grasshoppers (4 times higher), ants (2 – 12 times higher), kangaroo rats and pocket mice (3 – 12 times more Heteromyidae), and birds (1.5 – 3 times higher), and fewer crickets (almost none versus 5 – 8% of owl diets) than either Woodard (2002) or Marti (1974). For the remaining taxa, our results were similar to Marti (1974) but quite different from Woodard (2002), which suggests high variation but no long term changes. Compared to Woodard (2002), we found half the frequency of scarabs, 1/9 the long-horned beetles, 1/3 the camel crickets, 1/6 the Arachnids, and 1/8 the pocket gophers.

Overall, the proportion of insects in our burrowing owl diets was the same as Woodard (2002) and 4% lower than Marti (1974). We found 1.5 times the frequency of mammals as Woodard (2002) but half the frequency as Marti (1974). We counted more birds than either study: 1.5 times higher than Woodard (2002) and triple the frequency compared to Marti (1974). These data indicate that the same prey items continue to be consumed, but their proportions in owl diets on the PNG vary widely over time. Because burrowing owls are generalist predators, large changes in their diets probably do reflect changes in the actual abundance of prey taxa. Insects in particular can show large year to year fluctuations (Pfadt and Hardy 1987; McIntyre 2000; Crist 2008), but too much uncertainty exists to advocate a quantitative interpretation of these data (but see Johnson 1981; Marti 1987). The impact of burrowing owl predation on prey populations and the larger ecosystem are also unknown, but grasshopper predation may be important. Grasshoppers are considered the most important above ground insect herbivores in rangelands (Watts et al. 1982; Crist 2008) and may remove up to 25% of above ground biomass (Mitchell and Pfadt 1974; Hewitt and Onsager 1983).

Ecological Factors Associated with Prey Use

Owl diets responded strongly to rainfall, and breeding success was related to the relative proportions of mammals versus birds consumed. Results from prey remains largely corresponded to those for owl pellets, and indicators were found that explained the differences suggested by MRPP. Our first hypothesis was that owl prey use would vary among years, with a proportionally lower small mammal component in 2007 due to heavy summer rains. This hypothesis was supported, with large effects due to rainfall, which alternated between years during this study (Table 3.7). Spring rainfall showed the same alternating pattern as summer rainfall and they were highly correlated (Conrey unpub. data). During the driest year of our diet study (2006) when nest success and productivity were highest, more grasshoppers, more of many mammal species, and fewer birds were eaten, particularly horned larks (Tables 3.5a, 3.6a). Mammal consumption was particularly low in 2007, and it is possible that some small mammals may have drowned in burrows during large storm events in 2007, resulting in decreased abundance. However, changes in horned lark consumption seem unlikely to be related to their abundance, because their populations were relatively stable across wet and dry years (USGS Patuxent Wildlife Research Center 2010).

Some yearly patterns emerged that were not fully explained by rainfall: indicator taxa from the wetter years of 2005 and 2007 did not entirely correspond to one another (Tables 3.5a, 3.6a). We studied only the effects of spring – summer precipitation, at the time when owls are arriving and breeding, but some of the unexplained annual differences in owl diet might be accounted for if other climatic variables were examined. More years of data would help in understanding the role of winter precipitation, lag effects from previous years' precipitation (the dry years of our study both followed much wetter years: Table 3.7), and large storm events. During May – July in our study, storms showed a high correlation with total summer rainfall, so our wet/dry categories were unchanged by the addition of storm data: 2005 and 2007 each had five storms of which 2 – 3 were large (> 30 mm), while 2006 had three storms of which one was large. One storm in 2007 dropped 40 – 80 mm of rain across the western PNG, which is ~ 1/5 the total precipitation in an average year. Although precipitation is thought to be the primary climatic factor structuring shortgrass steppe ecology (Lauenroth and Sala 1992), the effects of temperature, which varies less than precipitation does from year to year, could also be examined if more years of data were available.

The importance of summer rainfall to burrowing owl breeding ecology was confirmed by our analyses of nest and fledging success (Conrey Ch. 4). Rainfall was the most important variable in both analyses. Burrowing owls do not hunt during large rainfall events, and raptors are generally less active in wet weather (Village 1986; Woodard 2002). One would expect fewer captures of prey that live farther from nests in wet weather. If off-town vertebrates are an important prey source, then nestlings might starve or at least show declining body condition during extended wet periods (Wellicome

2000; Griebel and Savidge 2003). More years of data might show annual patterns independent of rainfall, but our breeding success data did not support yearly differences when rainfall levels were similar among years.

Second, we hypothesized that owl prey use would vary among prairie dog towns with different levels of prairie dog activity and time since plague. This hypothesis was not supported for any prey taxa except possibly for birds (Tables 3.3 – 3.6). Horned larks are most abundant in areas with heavy summer grazing (Giezentanner 1970; Wiens 1973), and in our study, consumption of horned larks increased with time since plague as prairie dog numbers recovered. Although lark buntings prefer lightly grazed or ungrazed areas (Wiens and McIntyre 2008), consumption by owls was very low on extinct towns. It is possible that burrowing owls do not travel as far from the nest to forage for birds, so town-level effects such as plague might be more relevant for avian prey. Prey availability differs on active and inactive towns (Bangert and Slobodchikoff 2006; Stapp 2007), probably because prairie dogs change the vegetation, including its height, species composition, and biomass (Hardwicke 2006; Hartley 2006; Hartley et al. 2009). Plague did influence the density and success of burrowing owl nests (Conrey Ch. 4). However, our prey composition data suggested that these differences were not associated with dietary changes, except possibly for avian prey. The lack of an effect on other prey taxa is probably related to how often owls forage off prairie dog towns, making town-level differences less important.

Third, we hypothesized that owl prey use would vary according to the density of owl nests, with fewer large prey items used where nest density was high. This hypothesis was supported only for prey remains (not pellet samples) for lark buntings and some mammals, excluding kangaroo rats (Table 3.6b). Perhaps there was more competition for rodents on upland sites and nearer nests, so owls nesting at higher densities spent more time foraging for kangaroo rats off towns. Overall, there is little evidence that owl nest density creates food limitation that might affect owl breeding success on the PNG (Conrey Ch. 4).

Fourth, we hypothesized that successful nests, particularly those with high productivity (at least four fledglings), would use a higher proportion of vertebrate prey, especially rodents. This hypothesis was supported for rodent prey, but we did not predict that birds would be associated with nest failure (Tables 3.4, 3.5b, 3.6b; Fig. 3.4b, c). Although insects were not associated with owl breeding success, grasshoppers were consumed more during 2006 when owl productivity was high. Owls probably took advantage of grasshopper abundance in 2006 and benefited from foraging on this accessible, and compared to other insects, high biomass food source. Vertebrates may have higher moisture and protein content than invertebrates (Pezzolesi 1994). Mammals made up 67% of the biomass consumed by burrowing owls in our sample (Table 3.1), and they have high individual biomass compared to insects (Fig. 3.2) or birds (Fig. 3.3). One possible explanation for our findings comes from optimal foraging theory, which predicts that predators will choose prey with the highest ratio of energetic benefit to foraging cost (MacArthur and Pianka 1966). It is possible that some pairs focused on avian prey with a lower nutritional reward per foraging effort compared to mammals, and that these pairs tended to be unsuccessful in fledging offspring.

However, it is also likely that burrowing owls turn to avian prey when mammals are harder to find in years when nest and fledging success are low. Of the three bird species commonly eaten by owls, only lark bunting abundance increased in wetter years (USGS Patuxent Wildlife Research Center 2010) when owls had poorer breeding success, so birds were more abundant only relative to mammals. Nevertheless, the relationship between bird consumption and decreased nest success may be correlative rather than causative. Most of the nest failure and owlet mortality that we observed could not be traced to a cause, but was likely a result of starvation, adult abandonment, shooting, non-badger predation, and collisions with vehicles. Of the 296 nest attempts we monitored from 2005 – 2007 (Table 3.7), two failed nests were dug out by badgers, one was flooded, one was trampled by cows, and one was disturbed by shooters who camped near the nest and shot for 3 days. One adult and three owlets at different nests were found after being shot, and one owlet was hit by a vehicle.

Considerations with Multivariate Analysis

Several considerations in this study included how to group samples and prey taxa and which multivariate analyses to use. One decision related to the level of specificity used in prey identification and analysis. We did not have the time or resources to go beyond the family level for invertebrate identifications, while identification to species was usually possible for vertebrates. Differences among insects could have been washed out by lumping genera or species into family-level groups if members of that family responded very differently to the independent variables being tested. However, we did find differences between invertebrate families that were correlated with year and rainfall. Numbers of many of the vertebrates in our samples were too small to allow them to be tested separately as species. We did our best to group species appropriately for analysis, for example, summing numbers of mammals that commonly live on upland prairie and prairie dog towns separately from those that do not. Differences among these groupings of vertebrate taxa were apparent for many of the variables that we tested, as were differences for classes and invertebrate families.

Entire textbooks (e.g., McCune and Grace 2002) have been written on multivariate analysis, and a large number of analytical methods have been developed. These tools are a natural choice for testing ecological hypotheses about prey species composition, because the composition data do not have to be lumped into such broad categories, such as rodents versus all other prey, as they would for univariate analysis. In addition, statistical tests are available that recognize the inherent lack of independence that exists when proportions of various items in the diet must sum to one, and these tests do not assume an underlying distribution or homogeneity of variances. We paired MRPP with indicator species analysis because they are easily interpreted and pair naturally: MRPP determined that prey species composition differed between groups organized according to ecological factors of interest, and ISA identified the prey taxa associated with each factor. MRPP and ISA had enough power to find differences between groups and identify taxa responsible for group differences.

Conclusion

Dietary information for owls is relatively easy to gather, although identification of small prey fragments is not easy. For any species, such information gives a greater understanding of community-level dynamics, and can be extended beyond lists of prey species consumed (fairly common in owl literature) to an exploration of ecological relationships among diet, abiotic factors, non-predatory interactions, and population dynamics (less common in the literature). Our results confirm the importance of precipitation in shortgrass steppe ecology, focusing on burrowing owls, a species 2 – 3 steps removed from primary production. However, the relationship was not as simple as might be expected; increased precipitation did not universally result in higher abundance of all species that consume vegetation and seeds (M. Lindquist pers. comm.; P. Stapp pers. comm.), nor did it lead to higher breeding success for burrowing owls (Table 3.7; Conrey Ch. 4). Some prey may have drowned, at least one owl nest was lost due to flooding, and owls were less active in wet weather. Overall, our results emphasize the wide variety of prey used by burrowing owls and the important relationships among rainfall, prey species composition, and owl breeding success.

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APPENDIX 1 – SOURCES OF INDIVIDUAL BIOMASS ESTIMATES

Table 3.8. Individual biomass estimates came from the literature and unpublished data. Sources were located as close as possible to our study site in northern Colorado.

Taxon	Citation	Location	Comments
Class Amphibia			
Ambystoma tigrinum	Feder (1988)	unknown	
Ambystoma tigrinum	Gray and Smith (2005)	Southern High Plains of TX	April - Sept. 1999 - 2000; adults
Spea bombifrons	Gray and Smith (2005)	Southern High Plains of TX	April - Sept. 1999 - 2000; adults
Class Arachnida			
Family Eremobatidae	Dickinson (unpub. data)	Pawnee National Grassland, Weld County, CO	June 1973
Class Aves			
Calamospiza melanocorys	Baldwin and Boyd (1973)	CO	May - Aug.
Calcarius mccownii	Giezentanner (1970)	Pawnee National Grassland, Weld County, CO	breeding adults
Eremophila alpestris	Maher (1972)	Matador, Saskatchewan, Canada	
Eremophila alpestris	Oberholser (1902)	unknown	
Eremophila alpestris	Wiens and Rotenberry (1980)	Jackson County, SD; Larson County, TX; Benton County, WA; Lake County, OR; Pershing County, NV	1970 - 1977, all seasons
Class Insecta			
Family Rhaphidophoridae			
Ceuthophilus longipes	Studier et al. (2002)	Carlsbad Caverns National Park, NM	May 1989
Ceuthophilus conicaudus	Studier et al. (2002)	Carlsbad Caverns National Park, NM	May 1989
Ceuthophilus carlsbadensis	Studier et al. (2002)	Carlsbad Caverns National Park, NM	May 1989
Hadenoecus subterraneus	Cyr et al. (1991)	Mammoth Cave National Park, KY	April 1986 - March 1987
All other families	Dickinson (unpub. data)	Pawnee National Grassland, Weld County, CO	April - Dec. 1970 - 1974
Class Malacostraca			
Orconectes peruncus	Riggert et al. (1999)	St. Francis River drainage, MO	Oct. 1996 - March 1998
Orconectes quadruncus	Riggert et al. (1999)	St. Francis River drainage, MO	Oct. 1996 - March 1998

Class Mammalia			
All species	Stapp (unpub. data)	Pawnee National Grassland, Weld County, CO	Sept. 1994 - 2008; averaged 80% adults, 10% subadults, 10% juveniles if weights available; otherwise, 85% adults and 15% subadults or 100% adults
Class Reptilia			
Coluber constrictor	Walton et al. (1990)	unknown	
Heterodon nasicus	Hill and Mackessy (2000)	AZ, CO	1997
Holbrookia maculata	Bonine and Garland (1999)	AZ and NM near Portal, AZ	1991, 1996
Holbrookia maculata	Bonine et al. (2001)	southern AZ and western NM near Portal, AZ; U.S. nationwide	May - early Aug. 1996 - 1997 and 1999; males
Phrynosoma hernandesi	Mathies and Martin (2008)	Pawnee National Grassland, Weld County, CO	June - Dec. 2005; adults
Phrynosoma hernandesi	Sherbrooke and Middendorf III (2001)	NM, AZ	June - Aug. 1988 - 1990; adult females and juveniles

APPENDIX 2 – OWL DIET COMPOSITION

Table 3.9. We identified 6774 prey individuals in owl pellets and 1348 prey individuals as remains, not counting 182 burrowing owl remains (mainly feathers) and 14 prairie dog remains (mainly toes and claws). These were unlikely to be prey, but were instead shed owl feathers, several owls that had been shot or died of other causes, and remains of prairie dogs that had probably died from plague or non-owl predation. Counts of higher level taxa are inclusive of taxa below them; for example, the six Squamata are the same six individuals listed as Class Reptilia. Items in owl pellets were consumed, while prey remains were unconsumed parts of prey individuals such as feathers, legs, or tails.

Latin Name	Common Name	# in Pellets	# in Remains
Class Amphibia	amphibians	4	14
Order Anura	frogs, toads	4	10
Family Pelobatidae	spadefoot toads	0	5
Spea bombifrons	plains spadefoot toad	0	5
Order Caudata	salamanders	0	4
Family Ambystomatidae	mole salamanders	0	4
Ambystoma tigrinum	tiger salamander	0	4
Class Arachnida	arachnids	22	2
Order Araneae	spiders	2	2
Order Solifugae	windscorpions	20	0
Family Eremobatidae	straight-faced windscorpions	20	0
Eremobates	sun spiders, windscorpions	6	0
Class Aves	birds	84	328
Order Caprimulgiformes	frogmouths	0	2
Family Caprimulgidae	nightjars	0	2
Chordeiles minor	common nighthawk	0	1
Phalaenoptilus nuttallii	common poorwill	0	1
Order Charadriiformes	plovers, terns	0	6
Family Charadriidae	plovers	0	6
Charadrius montanus	mountain plover	0	5
Charadrius vociferus	killdeer	0	1
Order Passeriformes	passerines	70	314
Family Alaudidae	larks	28	168
Eremophila alpestris	horned lark	28	168
Family Emberizidae	sparrows and allies	8	127
Aimophila cassinii	Cassin's sparrow	0	3
Calamospiza melanocorys	lark bunting	6	85
Calcarius mccownii	McCown's longspur	2	34
Pooecetes gramineus	vesper sparrow	0	2
Spizella breweri	Brewer's sparrow	0	3
Family Icteridae	blackbirds	0	5

Euphagus cyanocephalus	Brewer's blackbird	0	2
Molothrus ater	brown-headed cowbird	0	2
Sturnella neglecta	western meadowlark	0	1
Order Strigiformes	owls	2	0
Family Strigidae	typical owls	2	0
Athene cunicularia	burrowing owl	2	0
Class Insecta	insects	6412	757
Order Coleoptera	beetles	4447	224
Family Carabidae	ground beetles	2369	93
Pasimachus elongatus	blue-margined ground beetle	104	20
Family Cerambycidae	long-horned beetles	55	6
Moneilema annulatum	cactus long-horned beetle	13	0
Family Chrysomelidae	leaf beetles	2	0
Leptinotarsa	potato beetles	1	0
Family Cicindelidae	tiger beetles	1	0
Family Curculionidae	weevils	83	2
Superfamily Elateroidea	click, firefly, soldier beetles	24	0
Family Histeridae	clown beetles	13	0
Family Meloidae	blister beetles	3	1
Family Scarabaeidae	scarab beetles	966	54
Phanaeus vindex	rainbow scarab	8	0
Family Silphidae	carrion beetles	103	6
Family Tenebrionidae	darkling beetles	779	57
Family Trogidae	hide beetles	4	1
Order Diptera	flies	25	0
Order Hemiptera	true bugs, cicadas, hoppers, aphids	12	0
Family Cicadellidae	leafhoppers	1	0
Family Coreidae	squash bugs	10	0
Family Naucoridae	creeping water bugs	1	0
Order Hymenoptera	bees, ants	452	3
Family Formicidae	ants	407	2
Family Halictidae	sweat bees	1	0
Order Lepidoptera	butterflies, moths	17	1
Family Pyralidae	pyralid (micro) moths	13	0
Family Sphingidae	sphinx moths	0	1
Order Neuroptera	lacewings	1	0
Family Mantispidae	mantisflies	1	0
Order Odonata	dragonflies, damselflies	2	0
Order Orthoptera	grasshoppers, crickets	1454	529
Family Acrididae	short-horned grasshoppers	1243	517
Family Gryllidae	true crickets	3	1
Family Rhaphidophoridae	camel crickets	201	11
Class Malacostraca	crabs, lobster, shrimp, pillbugs	3	27
Order Decapoda	crabs, lobster, shrimp	3	27
Family Cambaridae	cambarid crayfish	3	27
Class Mammalia	mammals	243	196
Order Lagomorpha	rabbits, hares, pikas	1	4
Family Leporidae	rabbits, hares	1	4

Order Rodentia	rodents	236	187
Family Geomyidae	pocket gophers	6	8
Thomomys talpoides	Northern pocket gopher	6	8
Family Heteromyidae	pocket mice, kangaroo rats	65	143
Chaetodipus hispidus	hispid pocket mouse	2	0
Dipodomys ordii	Ord's kangaroo rat	30	142
Perognathus	small pocket mice	32	1
Perognathus flavescens	plains pocket mouse	2	0
Perognathus flavus	silky pocket mouse	13	0
Family Muridae	mice, voles	97	18
Microtus	voles	19	11
Microtus ochrogaster	prairie vole	11	7
Microtus pennsylvanicus	meadow vole	1	3
Mus musculus	house mouse	2	0
Onychomys leucogaster	Northern grasshopper mouse	17	4
Peromyscus maniculatus	deer mouse	22	1
Reithrodontomys	harvest mice	19	1
Reithrodontomys megalotis	Western harvest mouse	6	0
Reithrodontomys montanus	plains harvest mouse	2	1
Family Sciuridae	squirrels	20	15
Cynomys ludovicianus	black-tailed prairie dog	1	0
Spermophilus	ground squirrels	19	15
Spermophilus tridecemlineatus	13-lined ground squirrel	18	15
Class Reptilia	reptiles	6	24
Order Squamata	lizards, snakes	6	23
Family Colubridae	colubrid snakes	2	11
Coluber constrictor	racer	0	2
Heterodon nasicus	Western hognose snake	0	3
Family Phrynosomatidae	phrynosomatid lizards	3	7
Holbrookia maculata	common earless lizard	2	1
Phrynosoma hernandesi	short-horned lizard	0	5
Total		**6774**	**1348**

CHAPTER 4

PLAGUE AND RAINFALL INFLUENCE BREEDING SUCCESS AND NEST DENSITY IN BURROWING OWLS

ABSTRACT

Introduced pathogens such as plague (*Yersinia pestis*) can have far-reaching effects on native ecosystems that go beyond the mortality of infected individuals. We investigated the effects of introduced plague on burrowing owls (*Athene cunicularia*) nesting in black-tailed prairie dog (*Cynomys ludovicianus*) burrows in northern Colorado. Prairie dogs experience high mortality from plague, and their colonies are periodically extirpated by outbreaks. Plague does not make owls sick, but they may be affected as unmaintained burrows collapse and become uninhabitable, vegetation grows taller, and the anti-predator benefits of prairie dog association are lost. From 2005 – 2008, we monitored 311 burrowing owl pairs on the Pawnee National Grassland. We analyzed the effects of rainfall, prairie dog town, and plague dynamics on nest fate, fledging success, and distances from each nest to its three nearest neighbors. Rainfall was the strongest predictor of nest and fledging success, with higher rainfall associated with lower breeding success. Nests were more likely to succeed when plague events were more recent, and they produced more fledglings on towns where any extirpation was brief, and prairie dogs were otherwise resident on site for a longer time. Nests were closest together on recently plagued towns where prairie dog activity had been nearly continuous for a long time and

recolonization was rapid. Although ubiquitous on active prairie dog towns, burrowing owls were nearly absent from towns that were not recolonized after plague epizootics. If conservation of burrowing owls is a primary goal, our results suggest that it will be more useful to preserve prairie dog habitat and connectivity between towns at a landscape scale than to intensively manage plague.

INTRODUCTION

Introduced pathogens have the potential for far-reaching effects on native ecosystems that go beyond the mortality of infected individuals. Plague caused by *Yersinia pestis*, a bacterium that is endemic to the semi-arid grasslands and plateaus of Asia and Africa, was introduced into western ports of the United States in 1899 (Dicke 1926; Link 1955; Antolin et al. 2002). Plague was first reported in northern Colorado around 1948 (Ecke and Johnson 1952). Disease has been reported from at least 76 species of mammals in the western U.S., with high mortality in black-tailed prairie dogs (*Cynomys ludovicianus*: Barnes 1993; Cully and Williams 2001). Epidemics typically wipe out entire colonies, so instead of living in extensive towns as they once did, prairie dogs exist in metapopulations of smaller towns that periodically go extinct and are recolonized (Antolin et al. 2002; Stapp et al. 2004).

Flea-borne transmission is involved in epizootics (Cully and Williams 2001; Gage and Kosoy 2005), and flea load on black-tailed prairie dogs of the Pawnee National Grassland (PNG) of northern Colorado peaked in February – March and again from September – October, coinciding with epizootics (Tripp 2007; Tripp et al. 2009). The progression of plague seems to slow in summer, possibly because higher temperatures are associated with lower flea survival and transmission potential of *Y. pestis* (Tripp 2007; Tripp et al. 2009). Plague moves through larger towns as coterie (family group) after coterie is infected, dies out, and its territory is absorbed by surviving coteries who are themselves infected (Tripp 2007). Prairie dog towns naturally expand in number and area in May when juveniles emerge, sometimes doubling in size mainly from births but also from the arrival of immigrants. They retract again in fall and winter (Hoogland 1995; D. Tripp pers. comm.).

Black-tailed prairie dogs are widely considered to be ecosystem engineers and keystone species (Miller et al. 1994; Kotliar et al. 1999; Kotliar 2000; Miller et al. 2000; but see Stapp 1998), and often support a unique and diverse community of plants and animals (Lomolino and Smith 2004; Smith and Lomolino 2004; Hardwicke 2006; Stapp et al. 2008). The effects of plague on most prairie dog associates are unknown. However, black-footed ferrets (*Mustela nigripes*), obligate predators of prairie dogs and residents on towns, can be extirpated by plague, either through loss of prey or directly from the disease if not vaccinated (Williams et al. 1994; Matchett et al. 2010). Mountain plovers (*Charadrius montanus*), avian associates of prairie dog towns in Colorado, showed quickly declining nest numbers (Augustine et al. 2008) and occupancy of towns (Dinsmore and Smith 2010) following plague epizootics.

Burrowing owls (*Athene cunicularia*) are small ground-dwelling raptors of the prairies. They can be active at any time of day, hunting a wide variety of insects, mammals (not typically prairie dogs), birds, and other prey (Conrey Ch. 3). In the northern United States and Canada, most populations are migratory, nesting in burrows dug by mammals such as prairie dogs and ground squirrels (Haug et al. 1993). Black-tailed prairie dog burrows in Colorado are used for nesting and refuge, and mounds are used as perches. Plague does not make owls sick, but they may be affected as unmaintained burrows collapse and become uninhabitable, vegetation grows taller, and the anti-predator benefits of prairie dog association are lost. These may include increased visibility from trimming of vegetation, alarm calling, and providing an abundant alternate prey source (Hoogland 1995). Burrowing owls are widely distributed on the prairies of North, Central, and South America, but they are a declining and protected species in many areas and are a state-listed threatened species in Colorado (Colorado Division of Wildlife 2007). Our primary goal was to investigate the effects of plague on breeding burrowing owls.

We identified three parameters that were key to understanding and quantifying breeding owl populations: nest fate, fledging success, and nest density. We studied nest abundance and density in addition to nest and fledging success, because overall productivity is higher when high breeding success per nest accompanies high abundance and density of nests on the landscape. Fledging is often defined as the time when fully-feathered juveniles first leave the nest (Steenhof and Newton 2007). However, the term is sometimes used in the literature to describe the age at first sustained flight or when some level of independence from parents has been attained. Nest density on prairie dog towns has been variously defined as the number of nests per town area (Hughes 1993; Desmond and Savidge 1996) or as its inverse, the spacing between nests. Distance to the nearest neighbor has been most commonly reported (Desmond and Savidge 1996; Griebel 2000; Woodard 2002). Following the consensus within the burrowing owl literature, we define *fledging* age as 35 – 42 d. At this age, owlets can fly reasonably well and feed themselves, although parents may still feed and defend them. *Nest fate* is binary: 1 (success) or 0 (failure). Success means that at least one owlet fledges from a given nest. *Apparent nest success* refers to the proportion of nests in a sample or population that are known to be successful. *Fledging success* is the number of fledglings per nest. *Nest distance* is the distance between neighboring nests. We analyzed distances from each nest to its three nearest neighbors.

We focused our analyses at the scale of prairie dog towns. Other studies have examined nest-level aspects of site selection, including vegetation, burrow lengths, numbers, density, and proportion of active to inactive burrows (e.g., MacCracken et al. 1985; Green and Anthony 1989; Hughes 1993; Plumpton and Lutz 1993; Desmond et al. 1995; Toombs 1997; Desmond and Savidge 1999; Ekstein 1999; Restani et al. 2001; Woodard 2002; Lantz et al. 2007). One of the most important mechanisms producing variation in owl nesting habitat across the PNG of northern Colorado is plague, because the loss of prairie dog towns changes both plant and animal community structure and unattended burrows eventually collapse. Precipitation was also quite variable during our study, with noticeable effects on plant growth that differed from year to year, and climate is known to influence the likelihood of plague epizootics (Stapp et al. 2004). In addition, it was important to account for the effects of precipitation in a multi-year study because precipitation is considered to be the most important environmental factor governing ecology on the shortgrass steppe (Lauenroth and Sala 1992), and it typically varies more from one year to the next than temperature (Doesken and McKee 1999; Pielke and Doesken 2008).

Bad weather limits prey availability, decreases foraging efficiency, and can reduce nest success and survival in raptors (Village 1986; Steenhof et al. 1997). Ronan (2002) reported high variation in rainfall during a 3-year study in California, and found that burrowing owl breeding success was highest in the driest year that followed a very wet year. Owlet mortality may increase during periods of heavy rain, especially when rainfall lasts for several days (Wellicome 2000; Griebel and Savidge 2003). Some prey populations may respond positively to increased rainfall, but burrowing owls curtail their foraging in wet weather. We investigated the effects of both spring (March – May during arrival and nest establishment) and summer (May – July during breeding) precipitation on nest fate, fledging success, and nest distances.

Several studies have found that owls prefer active to inactive prairie dog towns (e.g., Butts and Lewis 1982; Toombs 1997; Orth and Kennedy 2001; Sidle et al. 2001; Tipton et al. 2008), and conflicting results have been found regarding town size (Plumpton 1992; Hughes 1993; Plumpton and Lutz 1993; Pezzolesi 1994; Desmond and Savidge 1996; Toombs 1997; Griebel 2000; Woodard 2002). However, the effects on breeding owls of town age, town extirpation by plague, and time to recovery of prairie dogs are unknown. The U.S. Forest Service PNG has conducted owl counts since 1998, in addition to mapping prairie dog towns since 1981. Those data suggested that owl numbers across the PNG were generally tracking the increasing area occupied by prairie dogs (Conrey, unpub. data). Similarly, Desmond et al. (2000) found that owl numbers tracked prairie dog populations in the Nebraska panhandle. They observed a time lag in the response of owl numbers to prairie dog population declines due to control. Burrows in Oklahoma filled within 3 years of prairie dog removal via cultivation and poisoning

(Butts and Lewis 1982). However, Hoogland (1995) noted that burrowing owls seemed common in prairie dog towns that had recently declined due to poisoning or plague, which mirrored our own initial observations on the PNG.

To our knowledge, no one has studied the effects of plague on owl breeding success or nest density. We were interested in comparing the effects of current prairie dog town dynamics with past town history. Current dynamics included whether a town was active or inactive and slow or fast-growing, as well as its size. Town history included the time since the most recent plague epizootic and the time since the town was first colonized by prairie dogs. We reset the clock on a town if it was extirpated and remained extinct for ≥ 2 years.

Finally, we were interested in how owl nest density might affect breeding success. High density of nests has led to decreased nest success in some (Griebel and Savidge 2007) but not all studies (Rosenberg and Haley 2004). A decline in nest success might result from competition for food or satellite burrows, used for rest or refuge, or other factors related to nest predators or parasites.

To summarize, our objective was to examine the effects of rainfall, prairie dog, and plague dynamics on nest fate, fledging success, and nest density (indexed by mean distance to the three nearest nests). We tested the following hypotheses:

1. Nest fate, fledging success, and nest distance will vary from year to year, with lower nest and fledging success in wetter summers and higher nest distance in wetter springs. An alternative hypothesis is that breeding success will increase and nests will be closer together during wetter weather (if some prey respond positively: Conrey Ch. 3).

2. Plague epizootics will lead to increased nest and fledging success and decreased nest distances if towns are quickly recolonized by prairie dogs. Relative to younger towns, breeding success will be lower and nest spacing will be higher in towns that have been active for longer periods of time, and will be lowest in extinct towns, especially those that have had no prairie dogs for multiple years. An alternative hypothesis is that only current town dynamics matter. Regardless of when towns were colonized by prairie dogs or last experienced plague, towns that are smaller and fast growing (whether brand new or recently recolonized by prairie dogs) will have higher breeding success and more closely spaced nests than towns that are larger and more stable.
3. Owls nesting close to their neighbors will have lower breeding success.

If foraging and prey accessibility decline in wet weather, burrowing owls might be less likely to nest in wet springs and they may have nestlings in poorer condition during wet summers (Hypothesis 1: H1). Alternatively, if some prey respond positively to wet weather (Conrey Ch. 3), then the opposite pattern could occur (A1). Because burrowing owls prefer active towns, we expected extinct towns to have reduced nest density and breeding success (H2), especially after 2 years of inactivity (Butts and Lewis 1982). However, burrowing owls may prefer more heterogeneous environments (Orth and Kennedy 2001) and have higher nesting activity immediately after epizootics (Hoogland 1995). We predicted that recently plagued and recolonized towns would be preferred for nesting (more closely spaced nests) with high breeding success (H2). An alternative is that only current dynamics matter (A2), because both new and recently recolonized towns have similar dynamics. Competition may reduce breeding success in high density areas (H3).

METHODS

Study Site

Our study site (Fig. 4.1) on the Pawnee National Grassland (PNG) is located in the shortgrass steppe (SGS) of north central Colorado (Weld County). The SGS covers the central and southern Great Plains, the driest and warmest part of America's central grasslands (Lauenroth and Burke 1995; Pielke and Doesken 2008). The area managed by the USDA Forest Service PNG consists of 78,128 ha spread over a larger 50 x 100 km region with a patchwork of public and private ownership. We worked mainly in the northwestern PNG, which has mean elevation of 1650 m and mean annual precipitation of 321 mm, with > 70% of this falling as rain from April – September (National Climatic Data Center 2002; Pielke and Doesken 2008). The amount, timing, and intensity of precipitation are the most important factors in determining the ecology of the SGS (Lauenroth and Sala 1992). Most precipitation events on the PNG are small, with much of the water lost to evapotranspiration (Sala et al. 1992; Lauenroth and Bradford 2006). More than 80% of the PNG is upland steppe habitat (Hazlett 1998). The two dominant species are perennial C_4 warm-season grasses: blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*). Other common species are prickly-pear cactus (*Opuntia polyacantha*) and two dwarf shrubs: rabbitbrush (*Chrysothamnus nauseosa*) and saltbush (*Atriplex canescens*) (Lauenroth 2008).

Livestock grazing (mostly cattle) is the dominant land use across the PNG, and cattle were common on our study areas. Bird-watching and recreational shooting are also common on the PNG. Recreational shooting of legal and illegal targets occurred throughout the study period, and an 8.5-month open season (mid-June through February annually) on prairie dogs was reinstituted in June 2007 after a six-year moratorium. Extensive shooting occurred on several easily accessible towns, especially towns 51 and 78, with moderate shooting on all towns near gravel roads open to the public, and very little shooting on more isolated towns.

In a state-wide survey of Colorado, 80% of burrowing owl locations were on prairie dog colonies, and 24% of locations were in Weld County (VerCauteren et al. 2001). Burrowing owl occupancy in Colorado was highest on active prairie dog towns, followed by inactive towns, and all towns had much higher occupancy than grassland or dryland agriculture (Tipton et al. 2008). During three surveys of nine randomly-selected quarter sections (64.75 ha), we found only one nest that was not on a prairie dog town; another two off-town nests were discovered by chance. This compares to 320 nests located on prairie dog towns, which have been mapped by the Forest Service since 1981. The area occupied by these towns has increased since 1981 with an exponential increase since the mid-1990s. Declines in area occupied have occurred during recent plague epizootics, but due to rapid recolonization and the colonization of new towns, the total area occupied has remained around 1 – 2% of the PNG (Fig. 4.1).

Compared to adjacent uncolonized prairie, PNG prairie dog towns have more forbs, flowers, pollinator visits, and bare ground (Hardwicke 2006; Hartley 2006; Hartley et al. 2009). Total plant biomass is lower on older towns, and both young (< 7 yrs) and old towns have reduced grass biomass and a trend toward increasing forb biomass. Extirpated towns have similar plant biomass to uncolonized prairie (Hartley 2006; Hartley et al. 2009). Animal species associated with prairie dog towns include burrowing owls, mountain plovers (Dinsmore et al. 2005; Dreitz et al. 2005; Tipton et al. 2008), horned larks (*Eremophila alpestris*: Stapp et al. 2008), lesser earless lizards (*Holbrookia maculata*: Kretzer and Cully 2001), northern grasshopper mice (*Onychomys leucogaster*: Stapp et al. 2008), and desert cottontails (*Sylvilagus audubonii*: Stapp et al. 2008). Predator species including coyotes (*Canis latrans*), swift fox (*Vulpes velox*), and badgers (*Taxidea taxus*) often hunt on prairie dog towns (Stapp et al. 2008). We also regularly observed Swainson's hawks (*Buteo swainsoni*), Northern harriers (*Circus cyaneus*), and prairie falcons (*Falco mexicanus*) on towns, plus the occasional golden eagle (*Aquila chrysaetos*) and ferruginous hawk (*Buteo regalis*).

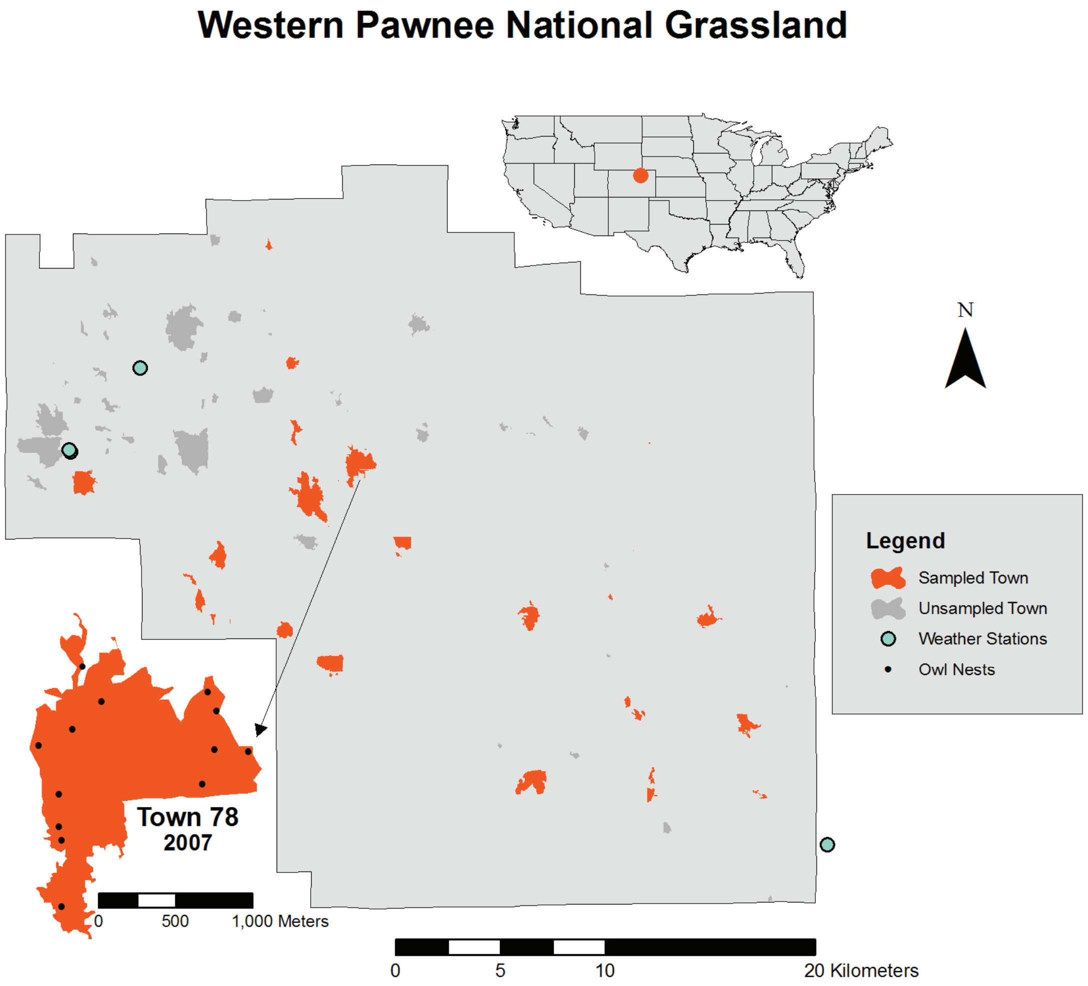

Figure 4.1. Prairie dog towns are displayed at their maximum extent for 2005 – 2008. In any given year, the total area occupied by prairie dog towns was approximately half the displayed area because of colonizations, extinctions, and other fluctuations in town size.

Nest Searches

We searched for adult owls on prairie dog towns and then looked for nest burrows in the vicinity of owl sightings. Early in the nesting season, adult males, who are not involved in incubation or brooding, typically perch conspicuously near the nest burrow during the day. Nest burrows were identified by the presence of shredded mammal manure (Levey et al. 2004), owl feathers, regurgitated pellets, and prey remains such as grasshopper legs, rodent tails, and passerine feathers. A burrow was identified as the site of a nest attempt only if shredded manure, typically cow, prairie dog, or canid, was present ("nest lining": Garcia and Conway 2009). Perching owls, whitewash (mutes), pellets, and prey remains were often seen at perch locations near a nest, but in our experience, shredded manure was present only at nests. Nest locations were recorded using UTM coordinates (Universal Transverse Mercator zone 13 NAD1983) with specified accuracy of 15 m but < 4 m accuracy of marked waypoints typical in the field.

We conducted a minimum of three complete surveys on each prairie dog town so that a removal method (Hayne 1949; Otis et al. 1978; White et al. 1982; Rosenberg and Haley 2004) could be used to estimate nest abundance and probability of nest detection. Positive bias (systematic overestimation of unknown magnitude) in apparent nest success (Mayfield 1960; 1961; 1975) is likely to be small when most nests are discovered early in the breeding season and nests are easy to detect (Lantz and Conway 2009). Our probability of detecting a nest in three surveys was > 95%, and we are confident that most if not all nests were discovered on monitored prairie dog towns. The removal method required a closed population of nests, so we began our surveys in mid-May after most owls had arrived and established, or begun to establish, their nests. We estimate that most nests were found during incubation, with smaller numbers found during the nestling (post-hatch) or egg-laying stage.

The number of nests per town was a covariate in our analyses of nest fate and fledging success. We predicted that pairs with more neighbors would have lower breeding success. We also tested a quadratic term because we thought the decline in nest and fledging success would level off with increasing nest numbers.

Monitoring Reproduction

Visual counts of the area surrounding each owl nest using spotting scopes produced an estimate of the minimum number of owlets known alive. We counted owlets for ≥ 15 min. at all nests and recorded the maximum number of owlets at each nest every 5 min. If we were unsure where an owlet belonged, we observed it until it moved to a nest, joined other owlets, or was fed by an adult. In the few cases (under five per year) where the nest could not be identified, the owlet was not counted. Each owlet was aged according to behavior, plumage characteristics, and size (Priest 1997). For analysis, owlets that could not be aged because our view was blocked or too brief were assigned the mean age for that nest. Presence of adults was noted, because lack of adult activity may indicate nest failure, as do prairie dogs in the burrow or cobwebs covering the entrance. Owl activity and visibility declined in poor weather, so we did not attempt to monitor nests in steady rain, hot (> 27°C), or windy (> 21 km/hr) conditions.

Nests were monitored once per week whenever possible, but the longest interval between observations was 13 days. We monitored each nest until all owlets at that nest were believed to be older than 50 days (d). Fledging of owlets at each nest may be staggered across a week or more, because females lay one egg every 1 – 2 days and usually begin incubation with the first egg (Bent 1938; Olenick 1990; Haug et al. 1993). Following Haug (1985) and Desmond and Savidge (1999), we used 42 d as fledging age, within the range of 35 – 44 d used by others (Thomsen 1971; Landry 1979; Todd et al. 2003; Davies and Restani 2006; Lantz and Conway 2009). Burrowing owl fledglings fly fairly well and are somewhat independent, as parental care such as feeding generally becomes less frequent after this age.

Logistics required that we consider an owlet to be fledged if observed at ≥ 35 d, because when nests are monitored once per week, owlets that have actually reached fledging age of 42 d are more likely to leave the nest area and remain undetected. Owlets within nests do not simultaneously reach 35 d, so while it would be ideal to count an owlet as fledged only if that particular individual was ≥ 35 d old, we could not age all owlets during each observation and considered all owlets as fledging at once from a particular nest with average age ≥ 35 d. Successful nests had at least one owlet known alive when average owlet age was ≥ 35 d. Fledging success per nest was equal to the largest number of owlets ever observed when average owlet age was ≥ 35 d.

We calculated apparent nest success rather than daily nest survival (Mayfield 1960; 1961; 1975; Johnson 1979; Stanley 2000; 2004; Dinsmore et al. 2002; Jehle et al. 2004) because we had imperfect knowledge of nest fate, and without a video probe, we could not always determine the stage of a nest or when a nest had failed prior to the end of the season. Lantz and Conway (2009), the only study of which we are aware that estimated daily nest survival for burrowing owls, found that positive bias in apparent nest success was only 3 – 6%. Based on our high probability of nest detection, we expect that positive bias was small in our study as well and likely balanced by a small amount of negative bias if fledged owlets were sometimes undetected.

Nest fate and fledging success were two of the three response variables modeled in this study. Each nest was considered a sampling unit.

Quantifying Nest Distance

Previous studies of spatial use by nesting burrowing owls (e.g., Hughes 1993; Desmond and Savidge 1996; Desmond et al. 2000; Griebel 2000; Woodard 2002) used either number of nests per study area to measure density or distance to the nearest (single) neighbor as an index inversely proportional to density. We did not estimate nest density with number of nests/prairie dog town area, because it was unclear what study area to use. The Forest Service's mapping of prairie dog towns did not necessarily correspond with the owl breeding season, and towns were constantly shrinking and expanding. It is difficult to accurately map prairie dog town boundaries from the ground, because edge burrows are easily missed, and most nests were near town edges (Fig. 4.1; Conrey, unpub. data). In addition, the Forest Service mapped only active burrows, and the town area they reported was zero for plagued towns. Following a plague event, inactive portions of towns might remain usable by burrowing owls, and the activity of just a few prairie dogs might be missed. For these reasons, some burrowing owl nests appeared to be outside of prairie dog town polygons.

The appropriateness of nearest neighbor statistics has been challenged in cases when other neighbors (aside from the nearest) have important interactions (Moilanen and Nieminen 2002). Because burrowing owl nests are clustered in space on prairie dog towns (Desmond et al. 1995; Desmond and Savidge 1996), nests may be relatively close to multiple neighbors (Fig. 4.1) and we wanted to quantify these potential interactions. We could not simply measure distances to all neighbors on a town, because solo nests do not have neighbors and averaging in a different number of neighbors for each nest would introduce unequal variances. Counting the number of neighbors within some radius of the focal nest just substitutes the choice of radius for the choice of number of neighbors. By averaging distances to the three nearest neighbors, we have accounted for the possibility of interactions with the majority of neighbors on an average town, which contained 6.06 nests. For towns with fewer than four nests, one or more of the measured distances connects to a neighbor on a different town. This greatly increases the average distance value but reflects the low density environment experienced by the focal nest.

We imported our nest locations into ESRI ArcGIS version 9 (ArcMap version 9.3.1: Environmental Systems Research Institute 2009) and created a separate point layer for each year. The distance from each nest to the three nearest nests was calculated using Hawth's Analysis Tools version 3.27 (Beyer 2006). This tool works within ArcMap to calculate distances among points within a dataset. It creates a full matrix of distances between points and can also be used to identify and measure distances from focal points to a user-selected number of nearest neighbors (up to 100).

Our measure likely has an inflated tail, with large distances for the most isolated nests because we did not attempt to find every nest on the PNG. Several nests on towns with fewer than four nests total may have had closer neighbors on private land than the ones that we identified on federal land. Eight nests (of 311) on four towns may have had closer neighbors on the few towns we could not survey. However, even if we mapped every owl nest on the western PNG, nests with few neighbors would have large mean distance values, because distances among towns occupying 1 – 2% of the PNG (Fig. 4.1) are very large relative to distances among nests within towns. We validated the robustness of our distance measure by testing for effects of number of neighbors: nests with at least three neighbors on a town vs. nests with fewer neighbors.

Nest distance was the third response variable modeled in this study. Each nest was considered a sampling unit. Nest distance was also used as a covariate in models of nest fate and fledging success. We tested a quadratic term, predicting that the benefit of being farther from neighbors would level off as distance increased.

Precipitation Data

We downloaded daily precipitation values from five weather stations (Fig. 4.1). Four were located on the Central Plains Experimental Range in the northwestern PNG. Three were located together: two (manual Station 11 and automatic Station 12) were administered by the SGS LTER, and one (CO22) was administered by the National Atmospheric Deposition Program. All three were included because one station may have missing data while the others are functioning, and different collection methods may cause variation in measurements. The fourth station on the CPER was administered by the USDA Agricultural Research Service and was located 5 km to the northeast. These four stations were at the northwest corner of our study area. The fifth station was located at Briggsdale at the southeast corner of our study area and was administered by the National Oceanic and Atmospheric Administration. We based our calculations of site-wide average daily precipitation value on the relative locations of these stations. Weights were as follows: Briggsdale (1/2), ARS (1/4), Station 11 (1/12), Station 12 (1/12), and CO22 (1/12). This system gave equal weight to stations at opposite corners of the study region: Briggsdale at one corner, and the other stations at the opposite corner, including Stations 11, 12, and CO22 at the same location.

These weighted precipitation data were positively correlated (Pearson's r = 0.899, t = 35.98, df = 309, $P < 2.2 \times 10^{-16}$) with spatially interpolated PRISM data (PRISM Climate Group, Oregon State University). Breeding season precipitation totals were 10.15 mm higher for our data, on average, compared to PRISM totals. However, we used data from four weather stations on the W PNG (1 km from the nearest prairie dog town) and from one station (Briggsdale) 500 m from the study area boundary (Fig. 4.1). PRISM used only the Briggsdale station, plus a number of more distant weather stations in Weld and surrounding counties. Because the nearest of these was > 19 km from the W PNG boundary and > 27 km from the nearest sampled prairie dog town, our data were probably more accurate, and the small differences between interpolated precipitation values would not have changed our characterization of wet and dry years. Spatial variation in rainfall across the W PNG cannot be accurately estimated until more stations exist with better spatial coverage.

Missing values led to underestimates in precipitation totals, so we filled missing values using average precipitation values for the nearby stations within our dataset; in such a dry area, many of the missing values were likely zeroes. If ≥ 14 days had missing values for a particular station within a given month, then that station was not used for calculation of that month's total precipitation.

We used the daily precipitation values to calculate monthly, seasonal, and annual totals. Spring precipitation totals were used to model nest distances, because owls arrive on the PNG and choose nest locations from March – May. Spring and summer breeding season (May – July) precipitation totals were both tested in models of nest fate and fledging success. In addition, we tested a binary variable (wet vs. dry), which constrained the wetter years (2005 and 2007) and the dryer years (2006 and 2008) to be equal. We hypothesized that higher rainfall would lead to lower breeding success and higher distances between nests.

Prairie Dog Town Data

The Forest Service has mapped prairie dog towns (Fig. 4.1) and reported on extinctions, colonizations, and the area occupied by active burrows since 1981. We classified towns based on their past and present prairie dog town dynamics. Current prairie dog town dynamics were categorized as extinct due to plague (no known prairie dogs), small with rapid growth, or large with slow growth. Small, rapidly growing towns averaged 9.2 ha with high prairie dog activity pushing the town boundary and relatively large year to year changes in area. Large, slowly growing towns averaged 70.8 ha with relatively small year to year changes in area. Alternate models constrained all active towns to be equal while allowing an offset for extinct towns, or constrained extinct and active towns to be equal while allowing an offset for growing towns. We predicted that growing towns would have the highest breeding success and lowest nest spacing, followed by long active and extinct towns.

We hypothesized that in addition to current town dynamics, plague and prairie dog colonization history would influence burrowing owl dynamics. We tested models that included the number of years since the most recent plague event and the number of years since the town was first initiated by prairie dogs, as early as 1981 when data were first collected. Our town initiation variable was the number of years in which a town had theoretically been continuously inhabitable by burrowing owls, meaning that prairie dogs had not been missing from the site for > 2 consecutive years since the town was initiated. Butts and Lewis (1982) reported that owls no longer nested on poisoned colonies after 3 years and were extremely reduced in number after 2 years. In wetter years on the PNG, we observed significant vegetative regrowth and exclusion of owls where vegetation was tall following just one year of extinction. We tested a quadratic term on plague year, predicting that the effects of plague would level off as time passed. We tested for quadratic and cubic effects of initiation year, predicting that nest spacing would initially shrink as owls began using a new town, and eventually increase and then level off as towns grew. We thought that breeding success might initially increase on new towns but would then decline or level off as time passed.

Finally, we tested the effect of town size. We attempted to account for the area actually usable by owls by using the maximum of the current and previous year's area. Towns may shrink or expand between the time that owls arrive and the Forest Service maps towns, and burrows may remain usable by owls even if they are not currently active. Inactive (no prairie dog use) portions of towns are not included in the Forest Service's size estimate, but they may remain usable by owls for a year or more before burrow systems begin to collapse. Our method accounted for this possibility in the year following a plague epizootic. We tested for quadratic effects of town size and cubic effects on breeding success, predicting that success would initially increase as small towns grew, but that this effect would be reversed or level off as towns became large and old. Nest distances were expected to be higher on larger towns, with this effect eventually leveling off due to the clustering tendencies of burrowing owls.

Generalized Linear Models

We built an *a priori* model set that included the precipitation, prairie dog town, and owl population variables described above. Because of the large number of variables being tested, we first ran single variable models. If these variables had some explanatory value, then we combined them into additive models. Models in the set were ranked using Akaike's Information Criterion (AIC: Akaike 1973) and coefficients were evaluated by examining their 95% confidence intervals. Because our sample size was large relative to the number of parameters in models, AICc (Burnham and Anderson 2002) produced almost identical results to AIC and only AIC is reported. We thought that rainfall might interact with other variables related to plague and prairie dog town dynamics. For example, plague might have a lower impact on habitat in a dry year than in a wet year when vegetation could grow quickly in the absence of prairie dogs. Similarly, differences between 1-year and 10-year old towns might partly depend upon climate, due to differential plant growth and interactions with prey species that might prefer wet or dry weather (Conrey Ch. 3).

We used generalized linear models (GLMs) to regress nest fate, fledging success, and nest distance on the explanatory variables of interest using the *glm* function in R version 2.8.1 (R Development Core Team 2008). GLMs are a class of models that generalize linear regression, allowing other error formulations if data are not normally-distributed. The linear model of explanatory variables is related to the response variable using an appropriate link function. In order to determine what form of GLM to use, we produced histograms of our data, considered what statistical processes produced the data, and chose the most appropriate link functions. Because each owl nest either succeeds with probability p or fails with probability $1 - p$, each nest represents a Bernoulli trial and the nest fate data are binomially distributed. We ran GLMs of the binomial family (logistic regression) with a logit link function.

The fledging success data are counts of fledglings per nest, so these are integer values with minimum value of zero. A histogram of the number of fledglings per nest appeared to be Poisson distributed, but with many more zero values than predicted by a Poisson model. The shape was a skewed bell curve peaking around 3, but with a second much higher peak at zero. Because Poisson distributions are bound by zero, it is common for count data to have inflated zero values. Our strategy with the fledging success data was to first fit a count model using a GLM of the Poisson family with a log link function. We then added a zero-inflation term that fit the excess zero counts using a binomial model with a logit link function. After modeling nest fate (zero fledglings vs. at least one fledgling), it became clear that a precipitation variable would be needed to adequately model the excess zeroes in the zero-inflated Poisson regression. Therefore, after some preliminary fitting of the count data, we added a zero-inflation term before continuing to run additive and interaction models on the count data. Zero-inflated poisson regressions used the *zeroinfl* function (Zeileis et al. 2008) in the pscl package (Jackman 2008) in R.

The nest distance data are continuous and bound by zero. The data appeared to be gamma distributed, with a very long tail of distances for the most isolated nests. We ran GLMs of the Gamma family with both inverse and log link functions. We had initially planned to use just the inverse link function, but five models failed to converge with the inverse link, and the signs on all beta coefficients were reversed (positive effects were negatively signed and vice versa). For models that converged with both link functions, results were very similar. After running all the models in our set, we checked the validity of our results by adding one additional variable. We knew that nest distances would be highly related to the number of nests on a town; if four nests occurred on a town, then all three nearest neighbors would be present on the same town and the mean distance would be smaller than on towns with fewer nests. We added a dummy variable for 4+ nests vs. fewer nests to determine whether our results would change significantly or if the top models would change position.

Several pairs failed and then renested in known locations nearby. For these pairs, only the renesting attempts were used in our breeding success models, because the eventual success or failure of these pairs depended on the fate of their renesting attempts. Only the original locations were used in models of nest distance, because the renest locations did not yet exist when owls were arriving on site and establishing nests. We could not use both locations in a given model, because two attempts by a single pair within a breeding season cannot be considered independent, especially when the first attempt always ended in failure.

We ran 29 nest fate models, 30 zero-inflated Poisson fledging success models, 26 nest distance models, and 5 validation models. We assessed goodness of fit by plotting residuals for the best-ranked model in each set and the general model in which it was nested. A sample of our R code is included in Appendix 1. The data are available at http://sgslter.colostate.edu/data_search.aspx.

RESULTS

Nesting and Plague

Burrowing owls were ubiquitous on active prairie dog towns, even in the first year following colonization of a new site. Only twice (two different towns in 2006) did we survey active towns with no burrowing owls. We surveyed five inactive towns, in which prairie dogs had been absent for ≥ 10 years as of 2005, on 11 occasions (and three surveys each) from 2005 – 2007. This yielded just one owl nest in an area where burrows had been kept open by badgers: a badger was seen and many burrow entrances were enlarged. In contrast, owls frequently nested on towns that had only recently experienced plague epizootics, in which prairie dogs had been absent for ≤ 1 year. Two towns plagued out in 2004 just prior to our study, nine plagued prior to the owl breeding season between 2005 and 2008, and one was poisoned by the Forest Service and then likely plagued but still had some prairie dogs as of summer 2008. All of these towns were recolonized by prairie dogs in ~ 1 year or less, and owls nested on all of them. This was true whether prairie dogs were present in early May when nests were established, or whether prairie dogs reoccupied the town later. However, the three towns that were extinct when owls established nests in May 2007 all lost nests relative to 2006. Towns that had already been recolonized by May (this occurred in each year of the study) gained nests on average over the previous year, and most owl nests were clustered in the small portions of the towns where prairie dogs were active.

Mean town size was 36.87 ha (40.37 SD) and ranged from 0.31 – 187.25 ha (Fig. 4.1). The mean number of owl nests on towns was 6.06 (4.44 SD: App. 2, Table 4.7). For towns that were surveyed in consecutive years, the mean change in nest number was

2.42 nests (3.80 SD, n = 12) gained from 2005 – 2006, 0.29 nests (3.59 SD, n = 24) lost from 2006 – 2007, and 3.00 nests (4.24 SD, n = 2) gained from 2007 – 2008. This annual change varied from a loss of nine nests to a gain of eight nests on two different towns. More nesting occurred during the dryer years when nest and fledging success were higher (2006 and 2008) relative to the wetter years when breeding success was lower (2005 and 2007).

We monitored 311 burrowing owl pairs nesting on 21 prairie dog towns (and two nesting off towns) over four years. Eleven pairs failed and renested in known locations, resulting in 322 total nest attempts. From 2005 – 2008, owlets were sighted in 1177 of 1989 total observations. The number of owlets counted per nest observation ranged up to twelve. Their ages varied from 8 – 85 d. Over four years, the date when the first owlets emerged from their nest burrows varied from the first to the third week of June. Most owlets fledged from late July to early August, but owlets from several renesting attempts did not fledge until September.

Nest Fate

Rainfall was by far the strongest predictor of nest fate (Table 4.1). Higher rainfall in 2005 and 2007 was associated with 62% nest success, compared to ~ 84% nest success in drier 2006 and 2008 (Table 4.2). Spring rainfall was highly correlated with summer rainfall, but summer rainfall was a better predictor of nest success. Rainfall levels were very similar in alternate years (Table 4.2), and performance of the binary variable (wet vs. dry) was quite close to that of the continuous variable.

Table 4.1. Nest Fate Models. Rainfall and years since the most recent plague event were the best predictors of nest fate.

Model	AIC	ΔAIC	Wt	Deviance	df	#Par
WetxPlagYr	355.60	0.00	0.25	347.60	300	4
Wet+PlagYr	356.05	0.45	0.20	350.05	301	3
Wet+PlagYr2	356.64	1.04	0.15	348.64	300	4
WetxPlagYr2	357.15	1.55	0.11	345.15	298	6
WetxPlagYr+Grow	357.34	1.74	0.10	347.34	299	5
Wet+Grow+PlagYr	357.78	2.19	0.08	349.78	300	4
Wet	360.07	4.47	0.03	356.07	309	2
Rain	360.73	5.13	0.02	356.73	309	2
Wet+Grow	360.88	5.28	0.02	354.88	308	3
WetxGrow	361.09	5.49	0.02	353.09	307	4
SprRain	361.71	6.11	0.01	357.71	309	2
Rain+SprRain	361.92	6.32	0.01	355.92	308	3
Y2005+Y2007	362.06	6.46	0.01	356.06	308	3
Year	363.57	7.97	0.00	355.57	307	4
PlagYr2	368.01	12.42	0.00	362.01	301	3
PlagYr	368.18	12.58	0.00	364.18	302	2
YrInit2	371.07	15.47	0.00	365.07	305	3
YrInit	371.43	15.83	0.00	367.43	306	2
YrInit3	372.01	16.41	0.00	364.01	304	4
Grow	374.14	18.54	0.00	370.14	309	2
Size3	375.84	20.24	0.00	367.84	307	4
Dyn	376.12	20.52	0.00	370.12	308	3
Dist3	376.66	21.06	0.00	372.66	309	2
Active	377.61	22.01	0.00	373.61	309	2
NumNests	377.82	22.22	0.00	373.82	309	2
Dist3_2	377.88	22.28	0.00	371.88	308	3
Size	378.19	22.59	0.00	374.19	309	2
Size2	378.78	23.18	0.00	372.78	308	3
NumNests2	379.76	24.16	0.00	373.76	308	3

Wet = wet (2005=2007) or dry (2006=2008). Rain = summer rainfall (mm). SprRain = spring rainfall. Year = 2005, 2006, 2007, or 2008. PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Dyn = current town dynamics (extinct, growing, or stable). Grow = growing or not (extinct=stable). Active = active or not. YrInit = years since town was initiated. YrInit2 = YrInit^2. YrInit3 = YrInit^3. Size = town size. Size2 = Size^2. Size3 = Size^3. Dist3 = mean distance to three nearest nests. Dist3_2 = Dist3^2. NumNests = number of nests on town. NumNests2 = NumNests^2.

Table 4.2. Breeding Success. Modeling of apparent nest success and fledging success for 311 owl pairs suggested that rainfall during the breeding season was the most important factor explaining differences among nests. The top models constrained the two wetter years to be different from the two dryer years (2005 = 2007 and 2006 = 2008). Fledging success is the number of owlets per nest. Means (SD) are shown.

Year	Summer Rainfall (mm)	Nest Success	Fledging Success (all nests)	Fledging Success (fate = 1)	Pairs
2005	168	62.3%	1.97 (2.08)	3.16 (1.78)	61
2006	97	82.4%	3.28 (2.56)	3.98 (2.27)	108
2007	150	61.5%	1.92 (2.12)	3.13 (1.88)	117
2008	80	88.0%	3.92 (2.18)	4.45 (1.71)	25
Overall	124	71.1%	2.56 (2.39)	3.61 (2.06)	311

Years since the most recent plague event also helped to explain the fate of nests on prairie dog towns (Table 4.1). On its own and in additive models, the plague year variable had a negative coefficient, meaning that nests on towns with more recent plague events were more likely to be successful (App. 3, Table 4.8). However, plague year was not significant in the interaction model (the top model: Table 4.1), and the 95% confidence intervals (CIs) overlapped zero for all models in the set (Table 4.3; App. 3, Table 4.8). Nevertheless, all models with ΔAIC < 2 included plague year, and models containing rainfall but not plague year had model weights < 4%. The effects of rainfall (Table 4.2) appeared to be stronger than any of the prairie dog town variables. The quadratic effect was not supported (Table 4.1), so plague effects on nest fate did not appear to level off with time.

None of the other town-level variables adequately modeled nest fate (Table 4.1; App. 3, Table 4.8). Distances from nests to their three nearest neighbors had no effect on their fate. Residuals from the top model (WetxPlagYr) and the more general model (WetxPlagYr2) were fairly small with no apparent trend except that the negative residuals associated with failures were somewhat larger in magnitude for the dry years.

Table 4.3. Coefficients of Top Models. Coefficients and 95% confidence intervals are shown for the top models in the analyses of nest fate (binomial), fledging success (count and zero-inflation coefficients), and nest distance (gamma).

Model	Type	Coeff	Estimate	SE	z_val	p	LCI	UCI
WetxPlagYr	Binomial	(Intercept)	1.428	0.271	5.265	0.000	0.918	1.988
	Binomial	wet	-0.726	0.352	-2.066	0.039	-1.429	-0.046
	Binomial	plagyr	0.034	0.035	0.969	0.333	-0.027	0.118
	Binomial	wetxplagyr	-0.055	0.038	-1.440	0.150	-0.142	0.013
Wet+YrInit_zWetxPlagYr	Count	(Intercept)	1.214	0.095	12.826	0.000	1.029	1.400
	Count	wet	-0.289	0.077	-3.738	0.000	-0.441	-0.138
	Count	yrinit	0.015	0.007	2.250	0.024	0.002	0.028
	Zero	(Intercept)	-1.538	0.299	-5.151	0.000	-2.123	-0.953
	Zero	wet	0.647	0.391	1.653	0.098	-0.120	1.414
	Zero	plagyr	-0.039	0.042	-0.942	0.346	-0.121	0.042
	Zero	wetxplagyr	0.062	0.044	1.388	0.165	-0.025	0.149
Dyn+PlagYr+YrInit2	Gamma	(Intercept)	7.416	0.347	21.349	0.000	6.779	8.106
	Gamma	dynext	0.157	0.373	0.422	0.674	-0.583	0.950
	Gamma	dyngrow	-0.316	0.209	-1.508	0.133	-0.733	0.082
	Gamma	plagyr	0.017	0.010	1.789	0.075	-0.002	0.037
	Gamma	yrinit	-0.212	0.039	-5.498	0.000	-0.289	-0.140
	Gamma	yrinit2	0.007	0.002	4.430	0.000	0.004	0.010

Wet = wet (2005=2007) or dry (2006=2008). PlagYr = years since most recent plague event. Dyn = current town dynamics (extinct, growing, or stable). YrInit = years since town was initiated. YrInit2 = YrInit^2.

Fledging Success

As with nest fate, rainfall was the strongest predictor of fledging success (Table 4.4). Increased rainfall in 2005 and 2007 was associated with fewer fledglings per nest compared to 2006 and 2008 (Table 4.2): 3.4 fledglings overall and 4 fledglings at successful nests in dry years versus 2 fledglings overall and 3.1 fledglings at successful nests in wetter years. Summer rainfall was a better predictor of fledging success than spring rainfall (Table 4.5). Again, performance of the binary variable (wet vs. dry) was almost identical to that of the continuous summer rainfall variable. In addition to explaining fledgling counts (Tables 4.3 – 4.5), rainfall also helped to model the excess zero counts associated with failed nests (Tables 4.3 – 4.4).

Table 4.4. Fledging Success Zero-Inflation Count Models. Rainfall and the number of years since towns were initiated by prairie dogs were the best predictors of fledging success. The first set of variables (e.g., Wet+YrInit) modeled fledgling counts, and the second set (e.g., zWetxPlagYr) modeled the excess zero counts.

Model	AIC	∆AIC	Wt	df	#Par
Wet+YrInit_zWetxPlagYr	1225.42	0.00	0.19	296	7
Wet+YrInit_zWet+PlagYr	1225.91	0.48	0.15	297	6
Wet+PlagYr+YrInit_zWet	1225.98	0.56	0.14	297	6
WetxYrInit_zWetxPlagYr	1226.93	1.51	0.09	295	8
Wet+PlagYr+YrInit_zWetxPlagYr	1226.98	1.56	0.09	295	8
Wet+PlagYr2+YrInit_zWet	1227.23	1.81	0.08	296	7
WetxYrInit_zWet+PlagYr	1227.39	1.97	0.07	296	7
Wet+PlagYr+YrInit_zWet+PlagYr	1227.44	2.02	0.07	296	7
Wet+PlagYr2+YrInit_zWetxPlagYr	1228.11	2.69	0.05	294	9
Wet+PlagYr2+YrInit_zWet+PlagYr	1228.69	3.26	0.04	295	8
Wet_zWetxPlagYr	1230.43	5.00	0.02	298	6
Wet_zWet+PlagYr	1230.84	5.42	0.01	299	5
Wet+PlagYr2_zWetxPlagYr	1231.14	5.72	0.01	296	8
Wet+PlagYr_zWetxPlagYr	1231.72	6.30	0.01	297	7
PlagYr2_zWet	1240.54	15.12	0.00	299	5
PlagYr_zWet	1241.73	16.31	0.00	300	4
Wet+YrInit_zWet	1248.88	23.46	0.00	303	5
Wet+YrInit_zWet+Grow	1249.93	24.51	0.00	302	6
WetxYrInit_zWet	1250.20	24.78	0.00	302	6
Wet+YrInit_zWet+YrInit	1250.37	24.95	0.00	302	6
Wet+YrInit_zWetxGrow	1250.56	25.14	0.00	301	7
Wet_zWet	1259.84	34.42	0.00	307	4
YrInit_zWet	1262.00	36.58	0.00	304	4
YrInit2_zWet	1263.68	38.26	0.00	303	5
Size3_zWet	1268.37	42.95	0.00	305	6
Size2_zWet	1270.96	45.54	0.00	306	5
NumNests2_zWet	1271.70	46.28	0.00	306	5
NumNests_zWet	1271.82	46.40	0.00	307	4
Size_zWet	1272.41	46.99	0.00	307	4
Grow_zWet	1274.90	49.47	0.00	307	4

Wet = wet (2005=2007) or dry (2006=2008). PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Grow = growing or not (extinct=stable). YrInit = years since town was initiated. YrInit2 = YrInit^2. Size2 = Size^2. Size3 = Size^3. NumNests = number of nests on town. NumNests2 = NumNests^2.

Table 4.5. Fledging Success Count Only Models. Summer rainfall was the best predictor of fledgling counts.

Model	AIC	∆AIC	Wt	Deviance	df	#Par
Wet	1409.88	0.00	0.38	742.55	309	2
Rain	1409.94	0.06	0.37	742.61	309	2
Year	1411.50	1.62	0.17	740.13	307	4
SprRain	1412.80	2.92	0.09	745.46	309	2
PlagYr2	1422.10	12.22	0.00	769.72	301	3
PlagYr	1428.79	18.92	0.00	778.42	302	2
Size3	1447.00	37.12	0.00	775.65	307	4
YrInit2	1447.40	37.52	0.00	780.73	305	3
YrInit	1448.60	38.72	0.00	783.91	306	2
Size2	1462.70	52.82	0.00	793.40	308	3
NumNests	1466.50	56.62	0.00	799.22	309	2
NumNests2	1466.90	57.02	0.00	797.61	308	3
Grow	1467.00	57.12	0.00	799.63	309	2
Dyn	1468.90	59.02	0.00	799.60	308	3
Dist3	1469.40	59.52	0.00	802.03	309	2
Dist3_2	1469.90	60.02	0.00	800.60	308	3
Size	1470.30	60.42	0.00	803.00	309	2
Active	1472.00	62.12	0.00	804.70	309	2

Wet = wet (2005=2007) or dry (2006=2008). Rain = summer rainfall (mm). SprRain = spring rainfall. Year = 2005, 2006, 2007, or 2008. PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Dyn = current town dynamics (extinct, growing, or stable). Grow = growing or not (extinct=stable). Active = active or not. YrInit = years since town was initiated. YrInit2 = YrInit^2. Size = town size. Size2 = Size^2. Size3 = Size^3. Dist3 = mean distance to three nearest nests. Dist3_2 = Dist3^2. NumNests = number of nests on town. NumNests2 = NumNests^2.

Older towns that had been initiated by prairie dogs a longer time ago had nests with higher fledgling counts on average (Tables 4.3 – 4.4). As parameterized, a town was continuously inhabitable by owls during this time because any inactive periods were < 2 years in duration. None of the other prairie dog town variables adequately modeled fledging counts (Tables 4.4 – 4.5; App. 3, Tables 4.9 – 4.10). The excess zeroes associated with nest failures were best modeled in the same way as in the nest fate model; both used binomial probabilities. Distances from nests to their three nearest neighbors had no effect on fledging success. No patterns were apparent in the residuals for either the top model (Wet+YrInit_zWetxPlagYr) or the more general model (WetxYrInit_zWetxPlagYr) when the data were sorted by plague or initiation year. The largest positive residuals were associated with the most productive nests, and the most negative residuals were associated with failed nests in dry years, but most were within four units of zero.

Nest Distance

Mean distance to the three nearest neighbors was 563.68 m (987.62 SD, range 61.41 – 7971.81 m) for nests on prairie dog towns and 308.91 m (348.59 SD, range 61.41 – 3647.93 m) for nests on towns containing at least four nests (where all three nearest neighbors were on the same town). Mean distance to the nearest neighbor was 249.61 m (588.92 SD, range 16.49 – 7567.66 m) for nests on prairie dog towns and 183.69 m (160.58 SD, range 18.18 – 1117.25 m) for nests on towns containing at least four nests.

Spring rainfall was unimportant in modeling the mean distance from each nest to its three nearest neighbors (Table 4.6). Year was a better predictor of nest distances than rainfall, but none of these variables produced good models (Table 4.6; App. 3, Table 4.11).

Table 4.6. Nest Distance Models. Years since the most recent plague event, time since prairie dog town initiation, and current town dynamics were the best predictors of nest spacing.

Model	AIC	ΔAIC	Wt	Deviance	df	#Par
Dyn+PlagYr+YrInit2	4302.71	0.00	0.67	257.72	297	6
Dyn+PlagYr2+YrInit2	4304.71	2.00	0.25	257.72	296	7
PlagYr+YrInit2	4307.39	4.68	0.06	264.30	299	4
PlagYr2+YrInit2	4309.34	6.63	0.02	264.26	298	5
Dyn+PlagYr2+YrInit	4329.18	26.46	0.00	278.26	297	6
Dyn+PlagYr+YrInit	4337.21	34.49	0.00	286.43	298	5
PlagYr2+YrInit	4354.18	51.47	0.00	302.45	299	4
PlagYr+YrInit	4354.72	52.01	0.00	304.65	300	3
Dyn+PlagYr2	4365.23	62.52	0.00	293.64	299	5
Dyn+YrInit2	4391.26	88.55	0.00	263.47	303	5
Dyn+PlagYr	4397.51	94.79	0.00	323.71	300	4
PlagYr2	4400.71	97.99	0.00	328.50	301	3
YrInit2	4416.64	113.93	0.00	286.47	305	3
YrInit3	4417.66	114.95	0.00	285.68	304	4
PlagYr	4419.54	116.83	0.00	348.33	302	2
YrInit	4456.39	153.67	0.00	322.22	306	2
Dyn	4573.21	270.50	0.00	376.97	308	3
Size2	4574.25	271.54	0.00	378.03	308	3
Active	4576.41	273.70	0.00	382.33	309	2
Size	4578.83	276.11	0.00	384.85	309	2
Grow	4587.76	285.05	0.00	394.27	309	2
Year	4592.76	290.05	0.00	395.34	307	4
SprRain	4593.10	290.39	0.00	400.00	309	2
Wet	4595.29	292.58	0.00	402.37	309	2
Y2005+2007	4595.43	292.71	0.00	400.35	308	3
Y2005	4597.99	295.28	0.00	405.31	309	2

PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Dyn = current town dynamics (extinct, growing, or stable). Grow = growing or not (extinct=stable). Active = active or not. YrInit = years since town was initiated. YrInit2 = YrInit^2. Size = town size. Size2 = Size^2. Year = 2005, 2006, 2007, or 2008. Wet = wet (2005=2007) or dry (2006=2008). SprRain = spring rainfall.

Nests were closer together on towns that had experienced more recent plague events (Tables 4.3, 4.6). The opposite trend occurred for the number of years since towns were initiated by prairie dogs. The distance between nests was smallest for nests on towns that had existed and been inhabitable by owls for a longer period of time, with a significant quadratic effect leading to a leveling off of this trend as years since town initiation increased (Tables 4.3, 4.6; App. 3, Table 4.11). The 95% CI around the coefficient for plague year slightly overlapped zero until either town dynamics (Dyn) or the quadratic term on initiation year (YrInit2) was removed from the model. However, both time since plague and town initiation were important explanatory variables: ΔAIC was > 60 whenever either town history variable was removed from the model.

In addition to variables describing prairie dog town history, current town dynamics were included in the two best models in the set, which had 92% of the model weight (Table 4.6). However, the coefficients that represented the offsets for growing and extinct towns from active towns were not significant in these two models, and their 95% CIs overlapped zero (Table 4.3). In higher AIC models, it appeared that nests were closer together on fast-growing towns and farther away on extinct towns, compared to older and more stable towns (Table 4.6; App. 3, Table 4.11).

These effects persisted when the binary variable differentiating nests with fewer than three neighbors on a town was included in models (App. 4, Table 4.12). The variables included in the top model did not change. The effect of town initiation date was not significant when the 4+ nest town variable was included in the model, but AIC increased by > 18 points and model weight declined to near zero when any of the town dynamics variables were removed from the model (App. 4, Table 4.12). Results for the inverse link function were generally parallel to those for the log link (App. 4, Table 4.13).

No other variables, including town size, were useful in modeling nest distances (Table 4.6; App. 3, Table 4.11). No trends associated with any of the independent variables that we tested were apparent in the residuals from the top or second-ranked more general model, although the residuals were larger for the most isolated nests. The tail of the distribution was too long for good model fit for these isolated nests with very large mean distance to the three nearest neighbors. To summarize, nests were closest together on recently plagued towns where prairie dog activity had been nearly continuous for a long time, apart from a brief absence prior to recolonization.

DISCUSSION

Influence of Precipitation

Our objective was to determine how climate and prairie dog – plague dynamics influence burrowing owl population dynamics. Summer rainfall was by far the strongest predictor of nest fate and fledging success (Tables 4.1 – 4.5). Apparent nest success was ~ 22% lower in wetter years, and fledging success dropped by ~ 1.4 owlets overall and one owlet at successful nests (Table 4.2). Our hypothesis that rainfall during the breeding season would reduce breeding success was supported over the alternative hypothesis that spring or summer rainfall would be beneficial. Summer rainfall was a better predictor of breeding success than spring rainfall (Tables 4.1, 4.4, 4.5), and the effects of increased rainfall were universally negative. More years of data might show annual patterns independent of rainfall, but our data showed that breeding success was similar among years with comparable summer rainfall.

Burrowing owls do not hunt during large rainfall events, and raptors are generally less active in wet weather (Village 1986; Woodard 2002). Nestlings may starve or at least show declining body condition during extended wet periods (Wellicome 2000; Griebel and Savidge 2003). Consumption of grasshoppers and some mammals was much higher in 2006 (a dry year) than in 2005 or 2007 (normal to wet years: Conrey Ch. 3).

Mammal consumption was associated with higher nest and fledging success, while bird consumption, which increased in wetter years, was associated with nest failure. Our prey use data indicated that foraging opportunities for mammals off prairie dog towns were probably important to productive nests, and owls may be unwilling to fly far from the nest in wet conditions. Only one nest was known to fail in 2007 as a direct result of flooding. Large portions of one prairie dog town flooded, and the water level was up to burrow entrances.

In contrast to our breeding success results, spring rainfall was unimportant in modeling the mean distance from each nest to its three nearest neighbors (Table 4.6). Year was a better predictor of nest distances than rainfall, but none of these variables produced good models (Table 4.6; App. 3, Table 4.11). However, nest numbers did change between wet and dry years. For towns that were surveyed in consecutive years, nest number per town declined from dry 2006 to wetter 2007, while the dryer years of 2006 and 2008 gained nests over the previous wetter years (App. 2; Table 4.7).

We studied only the effects of spring and summer precipitation, at the time when owls are arriving and breeding. This was likely the most important time of year to study, and most precipitation falls from April – September. However, additional years of data would help in understanding the role of winter precipitation or lag effects from previous years' precipitation; the dry years of our study both followed much wetter years. Large storm events might be particularly important to analyze, especially if one could model daily nest survival. During May – July in our study, storms showed a high correlation with total summer rainfall, so our wet/dry categories were unchanged by the addition of storm data: 2005 and 2007 each had five storms of which 2 – 3 were large (> 30 mm), while 2006 and 2008 each had three storms of which 0 – 1 were large. One storm in 2007 dropped 40 – 80 mm of rain across the western PNG, which is ~ 1/5 the total precipitation in an average year. Although the amount, timing, and intensity of precipitation are thought to be the primary climatic factors structuring shortgrass steppe ecology (Lauenroth and Sala 1992), the effects of temperature, which varies less than precipitation does from year to year, could also be examined if more years of data were available. Summer temperature and precipitation tend to be negatively correlated on the shortgrass steppe (Pielke and Doesken 2008).

Influence of Prairie Dog and Plague Dynamics

Colonization and extinction dynamics of prairie dog towns influenced burrowing owl use of towns, nest fate, fledging success, and nest distances. Only once did a pair nest on a town that had been inactive for many years. With only two exceptions in 2006, owls used every active prairie dog town that we surveyed as well as towns that had gone extinct due to plague within the past year. When beginning our field work, it appeared that owls nested at higher density and abundance on recently plagued and recolonized towns than on older, active towns. We therefore hypothesized that distances between nests would be lower on such towns. Frequent nesting on these post-plague towns suggested that breeding success might be higher relative to older, active towns that had not experienced plague events for a long time, although habitat use does not necessarily indicate habitat quality (Van Horne 1983).

This hypothesis was partly confirmed. The number of years since the most recent plague event helped to explain nest fate and nest distances (Tables 4.1, 4.3, 4.6; App. 3), but not fledgling counts (Tables 4.4 – 4.5). Nests were more likely to succeed and be closer to their neighbors on towns with more recent plague events. On its own and in additive models of nest fate, the plague year variable had a negative coefficient, meaning that nests on towns with more recent plague events were more likely to be successful (App. 3, Table 4.8). Although the 95% CIs for plague year overlapped zero (Table 4.1, 4.3; App. 3, Table 4.8), all models with ΔAIC < 2 included plague year, and models without this variable had model weights < 4%. Effect sizes suggest that the negative effects of rainfall were stronger than any of the prairie dog town variables in influencing breeding success.

Nests may be closer together after plague epizootics because owls want to occupy active portions of plagued and recolonized towns, and this portion has been reduced. Most owl nests were clustered in the small portions of towns where prairie dogs were active. However, the closer nest spacing observed after plague events was not entirely caused by the same number of nests packing into a smaller space; on average, plagued and recolonized towns gained 2.53 nests (4.05 SD) from the previous year, while all other towns either lost nests (extinct towns), remained stable (older active towns), or gained fewer nests (new towns).

When towns experience plague epizootics, heterogeneity on the town increases. Previous studies have found a positive relationship between breeding owls and landscape heterogeneity (Orth and Kennedy 2001), and nests tend to be close to colony edges (Toombs 1997; Ekstein 1999; Griebel 2000; Griebel and Savidge 2003; Teaschner 2005). One study cited higher owlet body condition (Griebel and Savidge 2003) near edges, but another found lower nest success (Ekstein 1999). We observed differential rates of vegetation regrowth within towns after epizootics, depending on rainfall and whether an area was in a hill or a swale. Heterogeneity was particularly pronounced when small numbers of prairie dogs were active in some parts of the town but not others, and we thought that a wider variety of prey might become available and benefit owls. However, we found little evidence that plague affects prey use (Conrey Ch. 3).

We did not predict the direction of the effect of town initiation year on fledging success and nest distances. On average, more owlets fledged from nests on towns where prairie dogs had been on site for a longer time (Tables 4.3 – 4.4), and nests were closer together (Tables 4.3, 4.6). There was no effect on nest fate. Years since town initiation was different from years since plague, because we did not reset the clock on a town unless prairie dogs were absent for 2 years. Older towns have more available burrows and more developed tunnel systems than younger towns, which may provide more potential nest locations, perches, satellite burrows, and refugia from predators or parasites. Following plague outbreaks, more of these burrows are empty and accessible to owls.

Increased burrow availability may be an important reason why owl nests tend to succeed on recently plagued towns and fledge more young on long occupied sites. We often observed adult owls successfully defending nests or perch mounds from prairie dogs who apparently wanted to reoccupy a burrow. One of the first signs that a nest had failed was the rapid reoccupation and digging activity of prairie dogs. However, owlets usually appeared uncertain of dominance relationships, so their use of satellite burrows may be curtailed where prairie dogs are abundant and actively using the majority of burrows.

Current town dynamics had some explanatory value for nest distances, but not for breeding success. These variables were included in the top ranked nest distance models with 92% of the model weight in the set (Table 4.6), but the 95% CIs around the coefficients for the top two models overlapped zero (Table 4.3). In other models, it appeared that nests were closer together on fast-growing towns and farther away on extinct towns, compared to older and more stable towns (Table 4.6; App. 3, Table 4.11). Given the explanatory power of the plague and initiation year variables, one reason that current town dynamics were not more helpful was the combination of new and recently recolonized towns into one class. Like plagued towns, brand new towns have less space available for nesting relative to older active towns, but fewer pairs may be aware of a new town and choose to nest there. In addition, new towns have fewer burrows overall, and therefore these nests may have fewer than three neighbors sharing the town and larger mean distance to the three nearest neighbors. If a plague epizootic occurs, a burrow system is already in place when prairie dogs reoccupy an existing site. This makes plagued and recolonized towns different from brand new towns or sites that were inactive for many years before recolonization. Prairie dog history on a site matters for nesting owls.

None of the other prairie dog dynamics variables were useful in modeling breeding success or nest distances. The lack of correspondence of town size with nest distances was surprising. Burrowing owls cluster their nests on prairie dog towns (Desmond et al. 1995; Desmond and Savidge 1996), so the correlation between nest distances and town size is not as tight as it would otherwise be. However, several studies have reported higher nest density on small colonies than large colonies (Hughes 1993;

Desmond and Savidge 1996; Woodard 2002). Although Stapp et al. (2004) found that small and large towns were more vulnerable to extinction than intermediate towns, the positive relationships that we observed between breeding owls, plague, and town age were unrelated to town size. Distances from nests to their three nearest neighbors had no effect on their fate or fledging success, nor did the total number of nests on a town.

Taken together, this suggests that burrowing owls are generally able to cluster their nests on the PNG without the penalty to their breeding success that might be expected from competition with neighbors (e.g., Griebel 2000). The reasons for clustering are unclear and may result from differential habitat quality across prairie dog towns or other habitat preferences. For example, the tendency to nest near edges of prairie dog towns may bring adults closer to prey that live off towns (Conrey Ch. 3). In addition, more burrows may be available near town edges when owls arrive in spring before prairie dogs have expanded back into foraging burrows and "summer homes" dug during the previous year (M. Antolin pers. comm.; D. Tripp pers. comm.). Clustering may also have a social benefit. It was not uncommon to observe association of owlets from different nests, especially for the youngest owlets late in the season when parental care was waning and both adults and older juveniles were spending more and more time farther from the nesting area. Several times we observed cooperation of adult owls who mobbed badgers.

Estimates of Breeding Success and Nest Distance

Most of the nest failure and owlet mortality that we observed could not be traced to a cause, but was likely a result of starvation, adult abandonment, shooting, non-badger predation, and collisions with vehicles. Of the 322 nest attempts we monitored from 2005 – 2008, two failed nests were dug out by badgers, one was flooded, one was trampled by cows, and one was disturbed by shooters who camped near the nest and shot prairie dogs and other targets for 3 days. Nest destruction by badgers was ruled out as the cause of failure in all other nest attempts, because their digging and major expansion of the burrow entrance is quite noticeable and easy to diagnose. One adult and three owlets at different nests were found after being shot, and one owlet was hit by a vehicle. Although debris from recreational shooting such as appliances and broken glass was common on some sites, and shot prairie dogs were found within 25 m of several owl nests, the effect of this disturbance on owls was difficult to determine in many cases.

Our estimates of apparent nest success were within the range reported by other researchers and were most similar to those from other prairie dog towns. We found 62 – 88% nest success (mean 71%) over 4 years. For studies of owls nesting on prairie dog towns, apparent nest success averaged ~ 74% and ranged from 52 – 92% (Plumpton 1992; Ekstein 1999; Lutz and Plumpton 1999; Griebel 2000; Restani et al. 2001; Woodard 2002; Griebel and Savidge 2007; Lantz and Conway 2009). For owls nesting elsewhere in other types of mammal burrows, agricultural areas, and urban areas, apparent nest success averaged ~ 58% and ranged from 41 – 85% (Haug 1985; Green and Anthony 1989; Olenick 1990; James et al. 1997; Mealey 1997; Wellicome et al. 1997; Lehman et al. 1998; Millsap and Bear 2000; Holmes et al. 2003; Conway et al. 2006) Nest success appears generally to be higher on prairie dog towns than in other habitats.

Our fledging success estimates were also within the range reported by other researchers. We counted 1.9 – 3.9 fledglings per nest (mean 2.6) over 4 years, and 3.1 –

4.5 fledglings per successful nest (mean 3.6). In previous studies on prairie dog towns, fledging success averaged ~ 2.6 owlets per nest (range 1.9 – 3.8), and 3.8 owlets per successful nest (range 3.5 – 5.3: Ekstein 1999; Lutz and Plumpton 1999; Desmond et al. 2000; Griebel 2000; Restani et al. 2001; Woodard 2002; Griebel and Savidge 2007). Fledging success in other habitats averaged ~ 3.0 owlets per nest (range 1.5 – 4.6) and 3.6 per successful nest (range 2.9 – 5.3: Wedgewood 1976; James et al. 1997; Mealey 1997; Conway et al. 2006). Although apparent nest success appears to be higher on prairie dog towns, fledgling counts are similar among habitats.

Much of the variation among studies likely has an environmental or biological cause, but some may also relate to differences in methods and frequencies of nest monitoring, unequal sightability of owlets (Conrey Ch. 2), and different definitions of fledging age. To facilitate comparisons with other studies and other species, we have presented results for the four owlet ages most commonly referenced in the literature as well as their behavioral progression (App. 5, Table 4.14).

Other studies have reported distances to the nearest single neighbor, but not to multiple neighbors. Desmond and Savidge (1996) measured mean nearest neighbor distance of 105.1 m on small prairie dog towns, and 125 m within nest clusters on large towns in Nebraska. Griebel (2000) found mean nearest neighbor distances of 266.7 – 296.3 m on towns in South Dakota. Nearest neighbor distance on active PNG prairie dog towns in 1999 – 2000 was 170.7 m (Woodard 2002); there was some overlap in sampled towns between our study and Woodard (2002). In our study, mean distance to the nearest neighbor was 249.6 m (588.9 SD, range 16.5 – 7567.7 m) on prairie dog towns and 188.3

m (164.7 SD, range 16.5 – 1117.3 m) within prairie dog towns containing more than one nest.

Summary and Implications

To summarize, rainfall was the strongest predictor of nest and fledging success. Nests were more likely to succeed when plague events were more recent, and they produced more fledglings on towns where prairie dogs had been resident for a longer time. Nests were closest together on recently plagued towns where prairie dog activity had been nearly continuous for a long time, aside from a brief absence following epizootics.

We observed a strong negative association of total summer rainfall with burrowing owl breeding success. However, it is likely that some nest failure and owlet mortality was caused by large storm events (acute rather than chronic effects: Village 1986; Wellicome 2000; Woodard 2002; Griebel and Savidge 2003). Climate scientists expect precipitation regimes to become more extreme in the future, with larger rainfall events separated by more extended dry periods (Easterling et al. 2000; Karl and Trenberth 2003; Goswami et al. 2006; Allan and Soden 2008; Groisman and Knight 2008). The consequences would extend beyond primary production (Knapp et al. 2008; Heisler-White 2009), and animal species may be affected in unexpected ways. Wildlife managers should be aware of potential impacts on burrowing owls and other dryland species.

Black-tailed prairie dogs provide the vast majority of nesting habitat for burrowing owls in Colorado (Orth and Kennedy 2001; VerCauteren et al. 2001; Tipton et al. 2008). Plague, an introduced pathogen that now occurs throughout much of the American shortgrass steppe, causes extirpation of prairie dog towns (Barnes 1993; Cully and Williams 2001; Antolin et al. 2002). Burrowing owls were ubiquitous on active prairie dog towns of the PNG, but were absent from towns that were not recolonized after plague epizootics. However, our results suggest that intensive management of plague is not advisable if the primary goal is burrowing owl conservation. As long as connectivity between towns is high enough to ensure high likelihood of rapid recolonization by prairie dogs, burrowing owls can adapt to plague and even benefit in some cases. Plague management via dusting for fleas or vaccination programs might be important on isolated prairie dog towns or when conservation of black-footed ferrets or mountain plovers is a priority. In other areas, it will be more useful to preserve prairie dog habitat and connectivity between towns at a landscape scale.

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APPENDIX 1 – R CODE

```
#################################################
### RUNNING BINOMIAL NEST FATE ANALYSIS ###
#################################################
success <- read.csv("regressiondata_success.csv", header=TRUE) #reads in data
head(success) #shows headers and first six rows
attach(success) #can now call column headings without naming variables

#Running Binomial Models#
SprRain = glm(fate ~ sprrain, family=binomial) #logistic regression
summary(SprRain) #displays output
AIC(SprRain)
confint_SprRain <- confint(SprRain) #95% confidence interval based on profile likelihood
# Make .csv Tables of Coeffs and Conf Ints #
outcoef_SprRain <- summary(SprRain)$coefficients
write.csv(outcoef_SprRain, "outcoef_SprRain.csv", row.names=T)
write.csv(confint_SprRain, "confint_SprRain.csv", row.names=T)


########################################################
### RUNNING POISSON FLEDGLING COUNT ANALYSIS ###
########################################################
success <- read.csv("regressiondata_success.csv", header=TRUE) #reads in data
head(success) #shows headers and first six rows
attach(success) #can now call column headings without naming variables

#Adding new columns modified from raw data#
plagyr2 <- plagyr^2 #creates new data
success <- cbind(success, plagyr2) #appends onto data frame

#Running Poisson Models#
PlagYr2 = glm(fledge ~ plagyr + plagyr2, family=poisson) #poisson regression
summary(PlagYr2) #displays output
AIC(PlagYr2)
confint_PlagYr2 <- confint(PlagYr2) #95% confidence interval based on profile likelihood
# Make .csv Tables of Coeffs and Conf Ints #
outcoef_PlagYr2 <- summary(PlagYr2)$coefficients
write.csv(outcoef_PlagYr2, "outcoef_PlagYr2.csv", row.names=T)
write.csv(confint_PlagYr2, "confint_PlagYr2.csv", row.names=T)
```

```
#Zero-Inflated Poisson Models#
# Count terms still modeled as Poisson with log link
# Zero inflation terms modeled as Binomial with logit link

#Running Zero-Inflated Poisson Models#
PlagYr2_zWet = zeroinfl(fledge ~ plagyr + plagyr2 | wet) #zero-inflated poisson regression
summary(PlagYr2_zWet) #displays output
AIC(PlagYr2_zWet) #displays AIC value
confint_PlagYr2_zWet <- confint(PlagYr2_zWet) #95% confidence interval
# Make .csv Tables of Coeffs and Conf Ints #
countcoef_PlagYr2_zWet <- summary(PlagYr2_zWet)$coefficients$count
zerocoef_PlagYr2_zWet <- summary(PlagYr2_zWet)$coefficients$zero
write.csv(countcoef_PlagYr2_zWet, "countcoef_PlagYr2_zWet.csv", row.names=T)
write.csv(zerocoef_PlagYr2_zWet, "zerocoef_PlagYr2_zWet.csv", row.names=T)
write.csv(confint_PlagYr2_zWet, "confint_PlagYr2_zWet.csv", row.names=T)


###################################################
### RUNNING GAMMA NEST DISTANCE ANALYSIS ###
###################################################
density <- read.csv("regressiondata_density.csv", header=TRUE) #reads in data
head(density) #shows headers and first six rows
attach(density) #can now call column headings without naming variables

Dyn = glm(dist3 ~ dynext + dyngrow, family=Gamma(link="log")) #gamma regression
summary(Dyn) #displays output
AIC(Dyn) #displays AIC value with more precision
gamma.shape(Dyn) #displays MLE of shape parameter
confint_Dyn <- confint(Dyn) #95% confidence interval based on profile likelihood
# Make .csv Tables of Coeffs and Conf Ints #
coef_Dyn <- summary(Dyn)$coefficients
write.csv(coef_Dyn, "coef_Dyn.csv", row.names=T)
write.csv(confint_Dyn, "confint_Dyn.csv", row.names=T)


##################
### RESIDUALS ###
##################
WetxPlagYr = glm(fate ~ wet + plagyr + wetxplagyr, family=binomial) #runs model
resid_WetxPlagYr <- WetxPlagYr$residuals #names residuals
write.csv(resid_WetxPlagYr, "resid_WetxPlagYr.csv", row.names=T) #outputs to file
```

APPENDIX 2 – OWL NESTS ON PRAIRIE DOG TOWNS

Table 4.7. Nests Per Year on Prairie Dog Towns. The number of burrowing owl nests on prairie dog towns varied by year. In several cases, the U.S. Forest Service Pawnee National Grassland assigned new numbers to towns that were recolonized after many years of inactivity, while we continued to use the original town number. We began monitoring two new towns before the Forest Service named them. The Forest Service did not survey prairie dog towns after three years of inactivity. We had more resources in 2006 and 2007 and were able to survey more towns. NS = not surveyed.

Pdog Town		**# of Nests**			
Conrey	FS	2005	2006	2007	2008
51	51	9	13	10	NS
53	NS	NS	0	0	NS
54	54	2	5	8	NS
62	62	9	9	2	NS
66	66	NS	0	4	NS
68	NS	0	0	0	NS
69	72	NS	4	5	NS
70	70	NS	0	5	NS
71	NS	1	0	1	NS
73	NS	NS	0	0	NS
74	74	10	15	6	6
75	NS	NS	0	0	NS
76	76	6	3	8	NS
77	92	NS	4	2	NS
78	78	8	12	13	19
79	79	5	2	2	NS
80	80	3	11	9	NS
81	81	NS	NS	17	NS
82	82	5	13	6	NS
83	83	2	6	5	NS
84	84	NS	2	5	NS
85	90	NS	3	1	NS
86	87	NS	1	2	NS
AN	99	NS	3	2	NS
EL	56,96	NS	1	4	NS

APPENDIX 3 – GLM COEFFICIENTS

Table 4.8. Binomial Nest Fate Analysis. Coefficients and 95% confidence intervals are shown for the analysis of nest fate (binomial) with a logit link function.

Model	Coeff	Estimate	SE	z_val	p	LCI	UCI
Year	(Intercept)	0.00328	0.00110	2.98568	0.00306	0.93266	3.43341
Year	y2005	-0.00201	0.00113	-1.77684	0.07658	-3.00678	-0.29670
Year	y2006	-0.00134	0.00114	-1.17443	0.24113	-1.95719	0.73822
Year	y2007	-0.00170	0.00113	-1.50650	0.13297	-3.00298	-0.39172
Rain	(Intercept)	3.20154	0.60515	5.29049	0.00000	2.05622	4.43737
Rain	rain	-0.01725	0.00431	-4.00632	0.00006	-0.02594	-0.00900
SprRain	(Intercept)	3.15070	0.60215	5.23242	0.00000	2.00558	4.37395
SprRain	sprrain	-0.02624	0.00668	-3.92859	0.00009	-0.03965	-0.01339
Wet	(Intercept)	1.61849	0.23337	6.93516	0.00000	1.18224	2.10165
Wet	wet	-1.13752	0.27975	-4.06618	0.00005	-1.70311	-0.60251
Dyn	(Intercept)	0.62509	0.20100	3.10995	0.00187	0.23770	1.02823
Dyn	dynext	-0.08610	0.51632	-0.16675	0.86757	-1.08014	0.97242
Dyn	dyngrow	0.49550	0.26433	1.87456	0.06085	-0.02419	1.01417
Grow	(Intercept)	0.61218	0.18512	3.30688	0.00094	0.25486	0.98259
Grow	dyngrow	0.50841	0.25247	2.01379	0.04403	0.01357	1.00510
Active	(Intercept)	0.53900	0.47559	1.13331	0.25708	-0.37160	1.52748
Active	active	0.38450	0.49297	0.77995	0.43542	-0.63375	1.33050

PlagYr	(Intercept)	1.08008	0.16881	6.39830	0.00000	0.75637	1.41942
PlagYr	plagyr	-0.02267	0.01216	-1.86429	0.06228	-0.04643	0.00136
PlagYr2	(Intercept)	1.27614	0.21859	5.83803	0.00000	0.85809	1.71706
PlagYr2	plagyr	-0.12428	0.06959	-1.78591	0.07411	-0.26043	0.01362
PlagYr2	plagyr2	0.00385	0.00259	1.48451	0.13767	-0.00130	0.00891
YrInit	(Intercept)	0.66329	0.26977	2.45875	0.01394	0.14040	1.20116
YrInit	yrinit	0.02357	0.02254	1.04568	0.29571	-0.02037	0.06822
YrInit2	(Intercept)	1.04647	0.37975	2.75572	0.00586	0.32706	1.82543
YrInit2	yrinit	-0.07452	0.06961	-1.07047	0.28441	-0.21707	0.05759
YrInit2	yrinit2	0.00464	0.00316	1.46607	0.14263	-0.00121	0.01134
YrInit3	(Intercept)	1.38102	0.51199	2.69734	0.00699	0.42114	2.44442
YrInit3	yrinit	-0.26158	0.19620	-1.33324	0.18245	-0.65504	0.11708
YrInit3	yrinit2	0.02458	0.01970	1.24773	0.21213	-0.01378	0.06369
YrInit3	yrinit3	-0.00055	0.00054	-1.03059	0.30273	-0.00161	0.00050
Dist3	(Intercept)	0.98419	0.14389	6.84010	0.00000	0.70662	1.27153
Dist3	dist3	-0.00014	0.00011	-1.25728	0.20865	-0.00035	0.00008
Dist3_2	(Intercept)	0.89509	0.17539	5.10342	0.00000	0.55350	1.24275
Dist3_2	dist3	0.00014	0.00034	0.40713	0.68391	-0.00050	0.00084
Dist3_2	dist3_2	0.00000	0.00000	-0.85823	0.39077	0.00000	0.00000
NumNests	(Intercept)	0.75249	0.26583	2.83074	0.00464	0.23755	1.28208
NumNests	numnests	0.01599	0.02595	0.61644	0.53761	-0.03453	0.06746
NumNests2	(Intercept)	0.66161	0.45628	1.44999	0.14706	-0.21594	1.58151
NumNests2	numnests	0.04023	0.10253	0.39235	0.69480	-0.16406	0.23928
NumNests2	numnests2	-0.00122	0.00499	-0.24438	0.80693	-0.01087	0.00877

Size	(Intercept)	0.90623	0.18301	4.95192	0.00000	0.55297	1.27168
Size	size	-0.00014	0.00245	-0.05905	0.95291	-0.00488	0.00478
Size2	(Intercept)	0.72372	0.23589	3.06810	0.00215	0.26920	1.19646
Size2	size	0.00868	0.00782	1.11015	0.26693	-0.00667	0.02403
Size2	size2	-0.00005	0.00004	-1.19329	0.23276	-0.00014	0.00003
Size3	(Intercept)	1.08307	0.29524	3.66840	0.00024	0.52060	1.68273
Size3	size	-0.02450	0.01707	-1.43534	0.15119	-0.05852	0.00858
Size3	size2	0.00047	0.00024	1.92099	0.05473	0.00000	0.00096
Size3	size3	0.00000	0.00000	-2.16731	0.03021	0.00000	0.00000
Rain+SprRain	(Intercept)	3.16000	0.61838	5.11016	0.00000	1.98697	4.42227
Rain+SprRain	rain	-0.05346	0.04160	-1.28497	0.19880	-0.14067	0.02347
Rain+SprRain	sprrain	0.05682	0.06466	0.87881	0.37951	-0.06375	0.19135
Y2005+Y2007	(Intercept)	1.61849	0.23337	6.93516	0.00000	1.18224	2.10165
Y2005+Y2007	X2005	-1.11640	0.35250	-3.16706	0.00154	-1.81408	-0.42675
Y2005+Y2007	X2007	-1.14848	0.30096	-3.81612	0.00014	-1.75240	-0.56861
Wet+Grow	(Intercept)	1.41643	0.29493	4.80264	0.00000	0.85711	2.01716
Wet+Grow	wet	-1.07363	0.28567	-3.75834	0.00017	-1.65002	-0.52614
Wet+Grow	dyngrow	0.28772	0.26362	1.09139	0.27510	-0.23106	0.80430
Wet+PlagYr	(Intercept)	1.64007	0.24519	6.68907	0.00000	1.18003	2.14546
Wet+PlagYr	wet	-1.04772	0.28896	-3.62586	0.00029	-1.63023	-0.49346
Wet+PlagYr	plagyr	-0.01073	0.01278	-0.83963	0.40112	-0.03563	0.01460
Wet+Grow+PlagYr	(Intercept)	1.49432	0.37159	4.02139	0.00006	0.78812	2.25010
Wet+Grow+PlagYr	wet	-1.03446	0.29010	-3.56593	0.00036	-1.61903	-0.47777
Wet+Grow+PlagYr	dyngrow	0.16953	0.32816	0.51662	0.60542	-0.48267	0.80828
Wet+Grow+PlagYr	plagyr	-0.00593	0.01579	-0.37591	0.70698	-0.03696	0.02514

WetxGrow	(Intercept)	1.85630	0.48088	3.86018	0.00011	1.00352	2.92982
WetxGrow	wet	-1.61335	0.52522	-3.07176	0.00213	-2.75494	-0.65736
WetxGrow	dyngrow	-0.32006	0.55021	-0.58171	0.56076	-1.49753	0.70077
WetxGrow	wetxdyngrow	0.82245	0.63246	1.30040	0.19346	-0.37170	2.13859
WetxPlagYr	(Intercept)	1.42822	0.27125	5.26532	0.00000	0.91850	1.98794
WetxPlagYr	wet	-0.72641	0.35162	-2.06590	0.03884	-1.42947	-0.04593
WetxPlagYr	plagyr	0.03420	0.03529	0.96894	0.33258	-0.02661	0.11770
WetxPlagYr	wetxplagyr	-0.05492	0.03814	-1.44012	0.14983	-0.14236	0.01272
WetxPlagYr+Grow	(Intercept)	1.28440	0.38951	3.29748	0.00098	0.54316	2.07599
WetxPlagYr+Grow	wet	-0.71377	0.35255	-2.02460	0.04291	-1.41848	-0.03127
WetxPlagYr+Grow	dyngrow	0.16795	0.32944	0.50981	0.61019	-0.48842	0.80793
WetxPlagYr+Grow	plagyr	0.03883	0.03641	1.06644	0.28622	-0.02483	0.12383
WetxPlagYr+Grow	wetxplagyr	-0.05480	0.03810	-1.43829	0.15035	-0.14218	0.01279
Wet+PlagYr2	(Intercept)	1.78920	0.27850	6.42446	0.00000	1.26432	2.36000
Wet+PlagYr2	wet	-1.02394	0.28971	-3.53438	0.00041	-1.60764	-0.46789
Wet+PlagYr2	plagyr	-0.09461	0.07135	-1.32604	0.18483	-0.23400	0.04685
Wet+PlagYr2	plagyr2	0.00316	0.00264	1.19536	0.23195	-0.00209	0.00832
WetxPlagYr2	(Intercept)	1.67826	0.34985	4.79713	0.00000	1.02075	2.40089
WetxPlagYr2	wet	-0.79203	0.45564	-1.73829	0.08216	-1.70213	0.09167
WetxPlagYr2	plagyr	-0.12982	0.13693	-0.94811	0.34307	-0.39027	0.15644
WetxPlagYr2	plagyr2	0.00685	0.00564	1.21465	0.22450	-0.00463	0.01818
WetxPlagYr2	wetxplagyr	0.02499	0.16079	0.15543	0.87648	-0.30317	0.33405
WetxPlagYr2	wetxplagyr2	-0.00373	0.00643	-0.57972	0.56210	-0.01650	0.00918

Wet = wet (2005=2007) or dry (2006=2008). Rain = summer rainfall (mm). SprRain = spring rainfall. Year = 2005, 2006, 2007, or 2008. PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Dyn = current town dynamics (extinct, growing, or stable). Grow = growing or extinct=stable. Active = active or not. YrInit = years since town initiated. YrInit2 = YrInit^2. YrInit3 = YrInit^3. Size = town size. Size2 = Size^2. Size3 = Size^3. Dist3 = distance to three nearest nests. Dist3_2 = Dist3^2. NumNests = number of nests on town. NumNests2 = NumNests^2.

Table 4.9. Zero-Inflated Poisson Fledgling Count Analysis. Coefficients and 95% confidence intervals are shown for the analysis of fledging success. Count coefficients are poisson (log link function) and zero-inflation coefficients are binomial (logit link).

Model	Type	Coeff	Estimate	SE	z_val	p	LCI	UCI
Wet_zWet	Count	(Intercept)	1.38562	0.04890	28.33566	0.00000	1.28977	1.48146
Wet_zWet	Count	wet	-0.29487	0.07643	-3.85810	0.00011	-0.44467	-0.14507
Wet_zWet	Zero	(Intercept)	-1.73617	0.25885	-6.70717	0.00000	-2.24351	-1.22883
Wet_zWet	Zero	wet	1.11199	0.31027	3.58389	0.00034	0.50386	1.72012
Grow_zWet	Count	(Intercept)	1.23658	0.06175	20.02485	0.00000	1.11555	1.35762
Grow_zWet	Count	dyngrow	0.02436	0.07738	0.31478	0.75293	-0.12730	0.17602
Grow_zWet	Zero	(Intercept)	-1.81806	0.27803	-6.53906	0.00000	-2.36299	-1.27313
Grow_zWet	Zero	wet	1.25283	0.32146	3.89731	0.00010	0.62278	1.88289
PlagYr2_zWet	Count	(Intercept)	1.34595	0.05780	23.28567	0.00000	1.23266	1.45923
PlagYr2_zWet	Count	plagyr	-0.04512	0.02411	-1.87156	0.06127	-0.09237	0.00213
PlagYr2_zWet	Count	plagyr2	0.00156	0.00086	1.80605	0.07091	-0.00013	0.00326
PlagYr2_zWet	Zero	(Intercept)	-1.81310	0.27909	-6.49654	0.00000	-2.36010	-1.26610
PlagYr2_zWet	Zero	wet	1.21959	0.32321	3.77339	0.00016	0.58611	1.85307
PlagYr_zWet	Count	(Intercept)	1.30306	0.04690	27.78602	0.00000	1.21115	1.39498
PlagYr_zWet	Count	plagyr	-0.00656	0.00401	-1.63720	0.10159	-0.01441	0.00129
PlagYr_zWet	Zero	(Intercept)	-1.75829	0.27289	-6.44309	0.00000	-2.29315	-1.22342
PlagYr_zWet	Zero	wet	1.18810	0.31837	3.73180	0.00019	0.56410	1.81209
YrInit_zWet	Count	(Intercept)	1.08570	0.08301	13.07954	0.00000	0.92301	1.24840
YrInit_zWet	Count	yrinit	0.01471	0.00630	2.33321	0.01964	0.00235	0.02707
YrInit_zWet	Zero	(Intercept)	-1.82391	0.28163	-6.47636	0.00000	-2.37589	-1.27193
YrInit_zWet	Zero	wet	1.22275	0.32534	3.75842	0.00017	0.58510	1.86040

YrInit2_zWet	Count	(Intercept)	1.12965	0.11231	10.05820	0.00000	0.90953	1.34978
YrInit2_zWet	Count	yrinit	0.00488	0.01798	0.27125	0.78620	-0.03037	0.04012
YrInit2_zWet	Count	yrinit2	0.00041	0.00069	0.59819	0.54971	-0.00094	0.00176
YrInit2_zWet	Zero	(Intercept)	-1.82622	0.28229	-6.46930	0.00000	-2.37949	-1.27294
YrInit2_zWet	Zero	wet	1.22423	0.32592	3.75619	0.00017	0.58543	1.86302
NumNests_zWet	Count	(Intercept)	1.12312	0.08240	13.62966	0.00000	0.96161	1.28462
NumNests_zWet	Count	numnests	0.01364	0.00762	1.79013	0.07343	-0.00129	0.02857
NumNests_zWet	Zero	(Intercept)	-1.80149	0.27367	-6.58270	0.00000	-2.33787	-1.26511
NumNests_zWet	Zero	wet	1.23095	0.31802	3.87069	0.00011	0.60765	1.85425
NumNests2_zWet	Count	(Intercept)	1.29685	0.14143	9.16940	0.00000	1.01965	1.57405
NumNests2_zWet	Count	numnests	-0.02996	0.03015	-0.99357	0.32043	-0.08905	0.02914
NumNests2_zWet	Count	numnests2	0.00210	0.00139	1.51070	0.13087	-0.00062	0.00482
NumNests2_zWet	Zero	(Intercept)	-1.79939	0.27313	-6.58808	0.00000	-2.33471	-1.26407
NumNests2_zWet	Zero	wet	1.22867	0.31754	3.86936	0.00011	0.60631	1.85104
Size_zWet	Count	(Intercept)	1.18581	0.05629	21.06679	0.00000	1.07549	1.29613
Size_zWet	Count	size100	0.11816	0.07270	1.62542	0.10407	-0.02432	0.26065
Size_zWet	Zero	(Intercept)	-1.82686	0.28006	-6.52308	0.00000	-2.37577	-1.27795
Size_zWet	Zero	wet	1.26176	0.32296	3.90681	0.00009	0.62876	1.89476
Size2_zWet	Count	(Intercept)	1.09642	0.07549	14.52349	0.00000	0.94846	1.24438
Size2_zWet	Count	size100	0.54640	0.24445	2.23523	0.02540	0.06729	1.02551
Size2_zWet	Count	size100_2	-0.26929	0.14815	-1.81768	0.06911	-0.55967	0.02108
Size2_zWet	Zero	(Intercept)	-1.81527	0.27683	-6.55732	0.00000	-2.35785	-1.27269
Size2_zWet	Zero	wet	1.24180	0.32081	3.87088	0.00011	0.61303	1.87057

Size3_zWet	Count	(Intercept)	1.20272	0.08844	13.59940	0.00000	1.02939	1.37606
Size3_zWet	Count	size100	-0.39780	0.50286	-0.79108	0.42890	-1.38339	0.58778
Size3_zWet	Count	size100_2	1.16820	0.68752	1.69915	0.08929	-0.17932	2.51572
Size3_zWet	Count	size100_3	-0.55034	0.25894	-2.12534	0.03356	-1.05785	-0.04282
Size3_zWet	Zero	(Intercept)	-1.82179	0.27872	-6.53620	0.00000	-2.36808	-1.27550
Size3_zWet	Zero	wet	1.23385	0.32326	3.81687	0.00014	0.60027	1.86743
Wet+YrInit_zWet	Count	(Intercept)	1.22838	0.08955	13.71686	0.00000	1.05286	1.40389
Wet+YrInit_zWet	Count	wet	-0.29519	0.07658	-3.85445	0.00012	-0.44530	-0.14509
Wet+YrInit_zWet	Count	yrinit	0.01397	0.00631	2.21542	0.02673	0.00161	0.02634
Wet+YrInit_zWet	Zero	(Intercept)	-1.73540	0.26091	-6.65139	0.00000	-2.24678	-1.22403
Wet+YrInit_zWet	Zero	wet	1.07081	0.31361	3.41451	0.00064	0.45616	1.68547
WetxYrInit_zWet	Count	(Intercept)	1.27947	0.10787	11.86084	0.00000	1.06804	1.49090
WetxYrInit_zWet	Count	wet	-0.41867	0.16861	-2.48310	0.01302	-0.74914	-0.08821
WetxYrInit_zWet	Count	yrinit	0.00964	0.00820	1.17534	0.23986	-0.00644	0.02572
WetxYrInit_zWet	Count	wetxyrinit	0.01054	0.01279	0.82442	0.40970	-0.01452	0.03560
WetxYrInit_zWet	Zero	(Intercept)	-1.73070	0.25990	-6.65915	0.00000	-2.24009	-1.22131
WetxYrInit_zWet	Zero	wet	1.06048	0.31337	3.38409	0.00071	0.44628	1.67468
Wet+YrInit_zWet+PlagYr	Count	(Intercept)	1.21491	0.09453	12.85166	0.00000	1.02962	1.40019
Wet+YrInit_zWet+PlagYr	Count	wet	-0.28835	0.07734	-3.72814	0.00019	-0.43995	-0.13676
Wet+YrInit_zWet+PlagYr	Count	yrinit	0.01474	0.00659	2.23768	0.02524	0.00183	0.02764
Wet+YrInit_zWet+PlagYr	Zero	(Intercept)	-1.77328	0.27541	-6.43859	0.00000	-2.31309	-1.23348
Wet+YrInit_zWet+PlagYr	Zero	wet	1.00701	0.32221	3.12534	0.00178	0.37549	1.63853
Wet+YrInit_zWet+PlagYr	Zero	plagyr	0.01150	0.01392	0.82674	0.40838	-0.01577	0.03878

Wet+YrInit_zWetxPlagYr	Count	(Intercept)	1.21414	0.09466	12.82585	0.00000	1.02860	1.39968
Wet+YrInit_zWetxPlagYr	Count	wet	-0.28914	0.07735	-3.73832	0.00019	-0.44074	-0.13755
Wet+YrInit_zWetxPlagYr	Count	yrinit	0.01483	0.00659	2.24996	0.02445	0.00191	0.02775
Wet+YrInit_zWetxPlagYr	Zero	(Intercept)	-1.53758	0.29851	-5.15089	0.00000	-2.12265	-0.95252
Wet+YrInit_zWetxPlagYr	Zero	wet	0.64685	0.39133	1.65294	0.09834	-0.12015	1.41385
Wet+YrInit_zWetxPlagYr	Zero	plagyr	-0.03912	0.04154	-0.94167	0.34636	-0.12055	0.04230
Wet+YrInit_zWetxPlagYr	Zero	wetxplagyr	0.06168	0.04444	1.38796	0.16515	-0.02542	0.14877
Wet+YrInit_zWet+Grow	Count	(Intercept)	1.22738	0.08971	13.68175	0.00000	1.05156	1.40321
Wet+YrInit_zWet+Grow	Count	wet	-0.29398	0.07657	-3.83931	0.00012	-0.44405	-0.14390
Wet+YrInit_zWet+Grow	Count	yrinit	0.01401	0.00632	2.21828	0.02654	0.00163	0.02639
Wet+YrInit_zWet+Grow	Zero	(Intercept)	-1.53783	0.32677	-4.70619	0.00000	-2.17829	-0.89738
Wet+YrInit_zWet+Grow	Zero	wet	1.01285	0.31996	3.16559	0.00155	0.38575	1.63995
Wet+YrInit_zWet+Grow	Zero	dyngrow	-0.28522	0.29268	-0.97451	0.32980	-0.85885	0.28842
Wet+YrInit_zWetxGrow	Count	(Intercept)	1.22914	0.08954	13.72656	0.00000	1.05364	1.40465
Wet+YrInit_zWetxGrow	Count	wet	-0.29514	0.07657	-3.85440	0.00012	-0.44522	-0.14506
Wet+YrInit_zWetxGrow	Count	yrinit	0.01392	0.00631	2.20498	0.02746	0.00155	0.02629
Wet+YrInit_zWetxGrow	Zero	(Intercept)	-1.96429	0.54486	-3.60514	0.00031	-3.03219	-0.89638
Wet+YrInit_zWetxGrow	Zero	wet	1.53544	0.59269	2.59061	0.00958	0.37378	2.69710
Wet+YrInit_zWetxGrow	Zero	dyngrow	0.30697	0.61921	0.49574	0.62007	-0.90666	1.52060
Wet+YrInit_zWetxGrow	Zero	wetxdyngrow	-0.80291	0.71053	-1.13003	0.25847	-2.19552	0.58969
Wet+YrInit_zWet+YrInit	Count	(Intercept)	1.23423	0.08959	13.77585	0.00000	1.05863	1.40983
Wet+YrInit_zWet+YrInit	Count	wet	-0.29508	0.07654	-3.85515	0.00012	-0.44510	-0.14506
Wet+YrInit_zWet+YrInit	Count	yrinit	0.01352	0.00633	2.13510	0.03275	0.00111	0.02593
Wet+YrInit_zWet+YrInit	Zero	(Intercept)	-1.53319	0.37983	-4.03654	0.00005	-2.27764	-0.78874
Wet+YrInit_zWet+YrInit	Zero	wet	1.06476	0.31295	3.40231	0.00067	0.45139	1.67814
Wet+YrInit_zWet+YrInit	Zero	yrinit	-0.01813	0.02545	-0.71240	0.47622	-0.06802	0.03176

Wet_zWet+PlagYr	Count	(Intercept)	1.39081	0.04969	27.98741	0.00000	1.29341	1.48821
Wet_zWet+PlagYr	Count	wet	-0.29508	0.07718	-3.82324	0.00013	-0.44636	-0.14381
Wet_zWet+PlagYr	Zero	(Intercept)	-1.75929	0.27204	-6.46694	0.00000	-2.29249	-1.22609
Wet_zWet+PlagYr	Zero	wet	1.01787	0.31825	3.19828	0.00138	0.39410	1.64163
Wet_zWet+PlagYr	Zero	plagyr	0.01158	0.01382	0.83837	0.40182	-0.01550	0.03866
Wet_zWetxPlagYr	Count	(Intercept)	1.39147	0.04962	28.04325	0.00000	1.29422	1.48872
Wet_zWetxPlagYr	Count	wet	-0.29621	0.07717	-3.83835	0.00012	-0.44747	-0.14496
Wet_zWetxPlagYr	Zero	(Intercept)	-1.52750	0.29587	-5.16273	0.00000	-2.10740	-0.94761
Wet_zWetxPlagYr	Zero	wet	0.66422	0.38750	1.71411	0.08651	-0.09527	1.42371
Wet_zWetxPlagYr	Zero	plagyr	-0.03734	0.04030	-0.92639	0.35424	-0.11633	0.04166
Wet_zWetxPlagYr	Zero	wetxplagyr	0.05977	0.04324	1.38228	0.16688	-0.02498	0.14452
WetxYrInit_zWet+PlagYr	Count	(Intercept)	1.26408	0.11576	10.91940	0.00000	1.03719	1.49098
WetxYrInit_zWet+PlagYr	Count	wet	-0.40270	0.17722	-2.27234	0.02307	-0.75003	-0.05536
WetxYrInit_zWet+PlagYr	Count	yrinit	0.01068	0.00867	1.23229	0.21784	-0.00631	0.02767
WetxYrInit_zWet+PlagYr	Count	wetxyrinit	0.00955	0.01329	0.71862	0.47237	-0.01650	0.03561
WetxYrInit_zWet+PlagYr	Zero	(Intercept)	-1.76798	0.27440	-6.44316	0.00000	-2.30579	-1.23017
WetxYrInit_zWet+PlagYr	Zero	wet	0.99663	0.32195	3.09562	0.00196	0.36562	1.62764
WetxYrInit_zWet+PlagYr	Zero	plagyr	0.01148	0.01393	0.82369	0.41012	-0.01583	0.03878
WetxYrInit_zWetxPlagYr	Count	(Intercept)	1.26242	0.11602	10.88143	0.00000	1.03503	1.48981
WetxYrInit_zWetxPlagYr	Count	wet	-0.40124	0.17743	-2.26134	0.02374	-0.74900	-0.05347
WetxYrInit_zWetxPlagYr	Count	yrinit	0.01086	0.00868	1.25100	0.21093	-0.00615	0.02787
WetxYrInit_zWetxPlagYr	Count	wetxyrinit	0.00936	0.01331	0.70340	0.48181	-0.01672	0.03544
WetxYrInit_zWetxPlagYr	Zero	(Intercept)	-1.53396	0.29761	-5.15419	0.00000	-2.11727	-0.95065
WetxYrInit_zWetxPlagYr	Zero	wet	0.63796	0.39135	1.63016	0.10307	-0.12907	1.40499
WetxYrInit_zWetxPlagYr	Zero	plagyr	-0.03857	0.04115	-0.93736	0.34857	-0.11922	0.04208
WetxYrInit_zWetxPlagYr	Zero	wetxplagyr	0.06112	0.04408	1.38672	0.16553	-0.02527	0.14752

Wet+PlagYr+YrInit_zWetxPlagYr	Count	(Intercept)	1.23329	0.09871	12.49445	0.00000	1.03983	1.42675
Wet+PlagYr+YrInit_zWetxPlagYr	Count	wet	-0.27859	0.07892	-3.53002	0.00042	-0.43327	-0.12391
Wet+PlagYr+YrInit_zWetxPlagYr	Count	plagyr	-0.00269	0.00409	-0.65912	0.50982	-0.01070	0.00532
Wet+PlagYr+YrInit_zWetxPlagYr	Count	yrinit	0.01445	0.00660	2.18913	0.02859	0.00151	0.02739
Wet+PlagYr+YrInit_zWetxPlagYr	Zero	(Intercept)	-1.53093	0.29790	-5.13916	0.00000	-2.11480	-0.94707
Wet+PlagYr+YrInit_zWetxPlagYr	Zero	wet	0.65241	0.38964	1.67439	0.09405	-0.11127	1.41609
Wet+PlagYr+YrInit_zWetxPlagYr	Zero	plagyr	-0.04081	0.04269	-0.95605	0.33905	-0.12448	0.04286
Wet+PlagYr+YrInit_zWetxPlagYr	Zero	wetxplagyr	0.06222	0.04545	1.36904	0.17099	-0.02686	0.15130
Wet+PlagYr2+YrInit_zWetxPlagYr	Count	(Intercept)	1.29352	0.11947	10.82738	0.00000	1.05937	1.52768
Wet+PlagYr2+YrInit_zWetxPlagYr	Count	wet	-0.27337	0.07911	-3.45534	0.00055	-0.42843	-0.11831
Wet+PlagYr2+YrInit_zWetxPlagYr	Count	plagyr	-0.02703	0.02748	-0.98356	0.32533	-0.08089	0.02683
Wet+PlagYr2+YrInit_zWetxPlagYr	Count	plagyr2	0.00093	0.00099	0.93935	0.34755	-0.00101	0.00286
Wet+PlagYr2+YrInit_zWetxPlagYr	Count	yrinit	0.01246	0.00700	1.78114	0.07489	-0.00125	0.02617
Wet+PlagYr2+YrInit_zWetxPlagYr	Zero	(Intercept)	-1.53143	0.29836	-5.13284	0.00000	-2.11620	-0.94666
Wet+PlagYr2+YrInit_zWetxPlagYr	Zero	wet	0.64649	0.39044	1.65579	0.09777	-0.11876	1.41174
Wet+PlagYr2+YrInit_zWetxPlagYr	Zero	plagyr	-0.04288	0.04430	-0.96784	0.33313	-0.12970	0.04395
Wet+PlagYr2+YrInit_zWetxPlagYr	Zero	wetxplagyr	0.06453	0.04687	1.37670	0.16860	-0.02734	0.15641
Wet+PlagYr_zWetxPlagYr	Count	(Intercept)	1.40992	0.05411	26.05572	0.00000	1.30387	1.51598
Wet+PlagYr_zWetxPlagYr	Count	wet	-0.28256	0.07879	-3.58611	0.00034	-0.43699	-0.12813
Wet+PlagYr_zWetxPlagYr	Count	plagyr	-0.00341	0.00409	-0.83426	0.40413	-0.01143	0.00461
Wet+PlagYr_zWetxPlagYr	Zero	(Intercept)	-1.51962	0.29514	-5.14889	0.00000	-2.09808	-0.94117
Wet+PlagYr_zWetxPlagYr	Zero	wet	0.67086	0.38553	1.74007	0.08185	-0.08478	1.42649
Wet+PlagYr_zWetxPlagYr	Zero	plagyr	-0.03936	0.04157	-0.94680	0.34374	-0.12084	0.04212
Wet+PlagYr_zWetxPlagYr	Zero	wetxplagyr	0.06039	0.04438	1.36096	0.17353	-0.02658	0.14737

Wet+PlagYr2_zWetxPlagYr	Count	(Intercept)	1.46742	0.06563	22.36039	0.00000	1.33880	1.59605
Wet+PlagYr2_zWetxPlagYr	Count	wet	-0.27411	0.07909	-3.46571	0.00053	-0.42913	-0.11909
Wet+PlagYr2_zWetxPlagYr	Count	plagyr	-0.04229	0.02575	-1.64205	0.10058	-0.09276	0.00819
Wet+PlagYr2_zWetxPlagYr	Count	plagyr2	0.00149	0.00093	1.60459	0.10858	-0.00033	0.00331
Wet+PlagYr2_zWetxPlagYr	Zero	(Intercept)	-1.52330	0.29639	-5.13955	0.00000	-2.10421	-0.94239
Wet+PlagYr2_zWetxPlagYr	Zero	wet	0.66003	0.38756	1.70303	0.08856	-0.09958	1.41963
Wet+PlagYr2_zWetxPlagYr	Zero	plagyr	-0.04242	0.04381	-0.96844	0.33282	-0.12828	0.04343
Wet+PlagYr2_zWetxPlagYr	Zero	wetxplagyr	0.06393	0.04639	1.37805	0.16819	-0.02700	0.15487
Wet+PlagYr+YrInit_zWet+PlagYr	Count	(Intercept)	1.23496	0.09871	12.51048	0.00000	1.04148	1.42843
Wet+PlagYr+YrInit_zWet+PlagYr	Count	wet	-0.27830	0.07871	-3.53599	0.00041	-0.43256	-0.12404
Wet+PlagYr+YrInit_zWet+PlagYr	Count	plagyr	-0.00277	0.00408	-0.67724	0.49825	-0.01077	0.00524
Wet+PlagYr+YrInit_zWet+PlagYr	Count	yrinit	0.01434	0.00659	2.17449	0.02967	0.00141	0.02726
Wet+PlagYr+YrInit_zWet+PlagYr	Zero	(Intercept)	-1.76343	0.27462	-6.42126	0.00000	-2.30169	-1.22518
Wet+PlagYr+YrInit_zWet+PlagYr	Zero	wet	1.00683	0.32147	3.13195	0.00174	0.37676	1.63690
Wet+PlagYr+YrInit_zWet+PlagYr	Zero	plagyr	0.01039	0.01409	0.73714	0.46104	-0.01723	0.03801
Wet+PlagYr2+YrInit_zWet+PlagYr	Count	(Intercept)	1.29138	0.11973	10.78561	0.00000	1.05671	1.52605
Wet+PlagYr2+YrInit_zWet+PlagYr	Count	wet	-0.27367	0.07880	-3.47284	0.00051	-0.42812	-0.11922
Wet+PlagYr2+YrInit_zWet+PlagYr	Count	plagyr	-0.02530	0.02707	-0.93433	0.35014	-0.07836	0.02777
Wet+PlagYr2+YrInit_zWet+PlagYr	Count	plagyr2	0.00086	0.00097	0.88247	0.37752	-0.00105	0.00277
Wet+PlagYr2+YrInit_zWet+PlagYr	Count	yrinit	0.01246	0.00699	1.78166	0.07480	-0.00125	0.02617
Wet+PlagYr2+YrInit_zWet+PlagYr	Zero	(Intercept)	-1.76846	0.27531	-6.42347	0.00000	-2.30806	-1.22886
Wet+PlagYr2+YrInit_zWet+PlagYr	Zero	wet	1.00799	0.32258	3.12473	0.00178	0.37574	1.64024
Wet+PlagYr2+YrInit_zWet+PlagYr	Zero	plagyr	0.01048	0.01408	0.74447	0.45659	-0.01712	0.03809
Wet+PlagYr+YrInit_zWet	Count	(Intercept)	1.23749	0.09858	12.55377	0.00000	1.04429	1.43070
Wet+PlagYr+YrInit_zWet	Count	wet	-0.27825	0.07866	-3.53739	0.00040	-0.43242	-0.12408
Wet+PlagYr+YrInit_zWet	Count	plagyr	-0.00315	0.00408	-0.77180	0.44023	-0.01113	0.00484
Wet+PlagYr+YrInit_zWet	Count	yrinit	0.01432	0.00659	2.17335	0.02975	0.00141	0.02724
Wet+PlagYr+YrInit_zWet	Zero	(Intercept)	-1.70470	0.26072	-6.53837	0.00000	-2.21571	-1.19369
Wet+PlagYr+YrInit_zWet	Zero	wet	1.05579	0.31403	3.36205	0.00077	0.44030	1.67128

Wet+PlagYr2+YrInit_zWet	Count	(Intercept)	1.29326	0.11951	10.82096	0.00000	1.05901	1.52750
Wet+PlagYr2+YrInit_zWet	Count	wet	-0.27356	0.07874	-3.47422	0.00051	-0.42788	-0.11923
Wet+PlagYr2+YrInit_zWet	Count	plagyr	-0.02548	0.02709	-0.94069	0.34686	-0.07858	0.02761
Wet+PlagYr2+YrInit_zWet	Count	plagyr2	0.00085	0.00097	0.87539	0.38136	-0.00106	0.00276
Wet+PlagYr2+YrInit_zWet	Count	yrinit	0.01247	0.00699	1.78480	0.07429	-0.00122	0.02616
Wet+PlagYr2+YrInit_zWet	Zero	(Intercept)	-1.70952	0.26182	-6.52941	0.00000	-2.22267	-1.19636
Wet+PlagYr2+YrInit_zWet	Zero	wet	1.05820	0.31512	3.35810	0.00078	0.44058	1.67582

Wet = wet (2005=2007) or dry (2006=2008). PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Grow = growing or not (extinct=stable). YrInit = years since town was initiated. YrInit2 = YrInit^2. Size = town size. Size2 = Size^2. Size3 = Size^3. NumNests = number of nests on town. NumNests2 = NumNests^2.

Table 4.10. Poisson Fledgling Count Analysis. Coefficients and 95% confidence intervals are shown for the analysis of fledging success (poisson with log link function).

Model	Coeff	Estimate	SE	z_val	p	LCI	UCI
Year	(Intercept)	1.36609	0.10102	13.52362	0.00000	1.16134	1.55775
Year	X2005	-0.68947	0.13615	-5.06402	0.00000	-0.95552	-0.42102
Year	X2006	-0.17893	0.11414	-1.56754	0.11699	-0.39817	0.04979
Year	X2007	-0.71217	0.12103	-5.88418	0.00000	-0.94598	-0.47096
Rain	(Intercept)	2.03587	0.13903	14.64319	0.00000	1.76169	2.30686
Rain	rain	-0.00874	0.00111	-7.85213	0.00000	-0.01093	-0.00656
SprRain	(Intercept)	2.05419	0.14559	14.10954	0.00000	1.76765	2.33854
SprRain	sprrain	-0.01377	0.00181	-7.61810	0.00000	-0.01733	-0.01024
Wet	(Intercept)	1.22333	0.04704	26.00842	0.00000	1.12970	1.31412
Wet	wet	-0.56157	0.07149	-7.85523	0.00000	-0.70219	-0.42184
Dyn	(Intercept)	0.83411	0.06312	13.21484	0.00000	0.70779	0.95531
Dyn	dynext	0.02812	0.16188	0.17370	0.86210	-0.30165	0.33446
Dyn	dyngrow	0.17301	0.07733	2.23735	0.02526	0.02265	0.32593
Grow	(Intercept)	0.83833	0.05812	14.42333	0.00000	0.72220	0.95012
Grow	dyngrow	0.16879	0.07331	2.30244	0.02131	0.02593	0.31343
Active	(Intercept)	0.86222	0.14907	5.78414	0.00000	0.55510	1.14084
Active	active	0.08376	0.15346	0.54580	0.58521	-0.20434	0.39867
PlagYr	(Intercept)	1.03971	0.04486	23.17759	0.00000	0.95064	1.12651
PlagYr	plagyr	-0.01307	0.00382	-3.41691	0.00063	-0.02068	-0.00568

PlagYr2	(Intercept)	1.14353	0.05630	20.31044	0.00000	1.03190	1.25265
PlagYr2	plagyr	-0.07552	0.02212	-3.41481	0.00064	-0.11968	-0.03295
PlagYr2	plagyr2	0.00240	0.00084	2.87166	0.00408	0.00079	0.00407
YrInit	(Intercept)	0.71873	0.08041	8.93779	0.00000	0.55916	0.87439
YrInit	yrinit	0.02045	0.00625	3.27305	0.00106	0.00819	0.03268
YrInit2	(Intercept)	0.85841	0.10920	7.86064	0.00000	0.63881	1.06713
YrInit2	yrinit	-0.01032	0.01809	-0.57027	0.56849	-0.04531	0.02566
YrInit2	yrinit2	0.00129	0.00071	1.80814	0.07058	-0.00013	0.00267
Dist3	(Intercept)	0.97639	0.04081	23.92601	0.00000	0.89568	1.05568
Dist3	dist3	-0.00006	0.00004	-1.65120	0.09870	-0.00014	0.00001
Dist3_2	(Intercept)	0.94126	0.05057	18.61440	0.00000	0.84108	1.03934
Dist3_2	dist3	0.00005	0.00010	0.49881	0.61792	-0.00015	0.00025
Dist3_2	dist3_2	0.00000	0.00000	-1.16436	0.24428	0.00000	0.00000
NumNests	(Intercept)	0.77740	0.07781	9.99153	0.00000	0.62312	0.92816
NumNests	numnests	0.01740	0.00721	2.41492	0.01574	0.00323	0.03148
NumNests2	(Intercept)	0.91775	0.13345	6.87689	0.00000	0.65095	1.17425
NumNests2	numnests	-0.01853	0.02904	-0.63806	0.52344	-0.07490	0.03899
NumNests2	numnests2	0.00175	0.00137	1.27636	0.20183	-0.00097	0.00441
Size	(Intercept)	0.88718	0.05235	16.94796	0.00000	0.78338	0.98861
Size	size	0.00097	0.00068	1.43078	0.15249	-0.00038	0.00228
Size2	(Intercept)	0.74113	0.07244	10.23137	0.00000	0.59676	0.88078
Size2	size	0.00766	0.00229	3.34691	0.00082	0.00320	0.01217
Size2	size2	-0.00004	0.00001	-3.02931	0.00245	-0.00007	-0.00001

Size3	(Intercept)	0.93818	0.08287	11.32174	0.00000	0.77252	1.09746
Size3	size	-0.00968	0.00467	-2.07166	0.03830	-0.01881	-0.00049
Size3	size2	0.00022	0.00006	3.50779	0.00045	0.00010	0.00035
Size3	size3	0.00000	0.00000	-4.18536	0.00003	0.00000	0.00000

Wet = wet (2005=2007) or dry (2006=2008). Rain = summer rainfall (mm). SprRain = spring rainfall. Year = 2005, 2006, 2007, or 2008. PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Dyn = current town dynamics (extinct, growing, or stable). Grow = growing or not (extinct=stable). Active = active or not. YrInit = years since town was initiated. YrInit2 = YrInit^2. Size = town size. Size2 = Size^2. Size3 = Size^3. Dist3 = mean distance to three nearest nests. Dist3_2 = Dist3^2. NumNests = number of nests on town. NumNests2 = NumNests^2.

Table 4.11. Gamma Nest Distance Analysis. Coefficients and 95% confidence intervals are shown for the analysis of nest distance (gamma with a log link function).

Model	Coeff	Estimate	SE	z_val	p	LCI	UCI
Year	(Intercept)	5.72017	0.33493	17.07858	0.00000	5.12843	6.45707
Year	X2005	0.94960	0.39769	2.38780	0.01755	0.11660	1.69652
Year	X2006	0.52585	0.37168	1.41479	0.15814	-0.26775	1.20752
Year	X2007	0.72773	0.36898	1.97226	0.04948	-0.06175	1.40271
Y2005	(Intercept)	6.30787	0.10952	57.59520	0.00000	6.10062	6.53049
Y2005	X2005	0.36190	0.24729	1.46345	0.14436	-0.10152	0.87318
Y2005+2007	(Intercept)	6.16603	0.14913	41.34565	0.00000	5.88732	6.47330
Y2005+2007	X2005	0.50373	0.26596	1.89403	0.05916	-0.00370	1.04503
Y2005+2007	X2007	0.28187	0.21800	1.29298	0.19699	-0.14508	0.71273
SprRain	(Intercept)	5.54192	0.41819	13.25215	0.00000	4.74088	6.38053
SprRain	sprrain	0.00991	0.00486	2.03700	0.04250	0.00036	0.01943
Wet	(Intercept)	6.16603	0.15078	40.89475	0.00000	5.88439	6.47686
Wet	wet	0.36356	0.19930	1.82420	0.06909	-0.03202	0.75174
Dyn	(Intercept)	6.43949	0.16689	38.58439	0.00000	6.12930	6.78545
Dyn	dynext	0.93271	0.43318	2.15316	0.03208	0.15477	1.88264
Dyn	dyngrow	-0.27734	0.21082	-1.31555	0.18930	-0.69930	0.13011
Grow	(Intercept)	6.64553	0.15594	42.61703	0.00000	6.35471	6.96755
Grow	dyngrow	-0.48338	0.20328	-2.37785	0.01802	-0.88785	-0.08831
Active	(Intercept)	7.37220	0.39803	18.52162	0.00000	6.68166	8.26844
Active	active	-1.09733	0.41078	-2.67136	0.00795	-2.01241	-0.37483

PlagYr	(Intercept)	5.99906	0.12018	49.91904	0.00000	5.76371	6.25093
PlagYr	plagyr	0.03062	0.00922	3.32068	0.00101	0.01163	0.05078
PlagYr2	(Intercept)	5.75779	0.13430	42.87208	0.00000	5.51672	6.01576
PlagYr2	plagyr	0.15226	0.04639	3.28239	0.00115	0.07298	0.23619
PlagYr2	plagyr2	-0.00471	0.00174	-2.70233	0.00728	-0.00789	-0.00171
YrInit	(Intercept)	6.84148	0.18336	37.31120	0.00000	6.54888	7.15254
YrInit	yrinit	-0.05689	0.01494	-3.80690	0.00017	-0.07984	-0.03349
YrInit2	(Intercept)	7.47334	0.22719	32.89409	0.00000	7.04927	7.94555
YrInit2	yrinit	-0.21026	0.03948	-5.32536	0.00000	-0.28889	-0.13663
YrInit2	yrinit2	0.00652	0.00166	3.92791	0.00011	0.00352	0.00979
YrInit3	(Intercept)	7.35813	0.29059	25.32101	0.00000	6.85176	7.93448
YrInit3	yrinit	-0.14314	0.11348	-1.26134	0.20815	-0.35541	0.05951
YrInit3	yrinit2	-0.00055	0.01137	-0.04847	0.96137	-0.02103	0.02040
YrInit3	yrinit3	0.00019	0.00031	0.62129	0.53487	-0.00036	0.00074
Size	(Intercept)	6.65389	0.13226	50.30802	0.00000	6.41277	6.91091
Size	size	-0.00567	0.00178	-3.19049	0.00157	-0.00880	-0.00236
Size2	(Intercept)	6.79440	0.17627	38.54463	0.00000	6.49226	7.12359
Size2	size	-0.01358	0.00577	-2.35296	0.01925	-0.02398	-0.00345
Size2	size2	0.00005	0.00003	1.51722	0.13024	-0.00001	0.00012
4Nests	(Intercept)	7.97207	0.11652	68.41524	0.00000	7.75206	8.20950
4Nests	X4nesttown	-2.32021	0.12414	-18.68981	0.00000	-2.57143	-2.08408
Dyn+PlagYr	(Intercept)	5.77162	0.26482	21.79411	0.00000	5.34045	6.23274
Dyn+PlagYr	dynext	1.13562	0.45264	2.50890	0.01264	0.35738	2.04524
Dyn+PlagYr	dyngrow	0.08507	0.25963	0.32767	0.74339	-0.35637	0.51446
Dyn+PlagYr	plagyr	0.03951	0.01239	3.18891	0.00158	0.01742	0.06259

Dyn+PlagYr2	(Intercept)	5.21497	0.24543	21.24839	0.00000	4.72050	5.69871
Dyn+PlagYr2	dynext	1.50277	0.38623	3.89085	0.00012	0.79187	2.29944
Dyn+PlagYr2	dyngrow	0.30130	0.21709	1.38789	0.16620	-0.11460	0.72469
Dyn+PlagYr2	plagyr	0.21501	0.04443	4.83914	0.00000	0.12961	0.30789
Dyn+PlagYr2	plagyr2	-0.00644	0.00160	-4.03212	0.00007	-0.00971	-0.00341
Dyn+YrInit2	(Intercept)	7.90827	0.24968	31.67314	0.00000	7.46371	8.38095
Dyn+YrInit2	dynext	-0.21913	0.32273	-0.67898	0.49767	-0.84331	0.49433
Dyn+YrInit2	dyngrow	-0.58299	0.14852	-3.92517	0.00011	-0.87215	-0.29893
Dyn+YrInit2	yrinit	-0.23918	0.03642	-6.56661	0.00000	-0.31047	-0.17123
Dyn+YrInit2	yrinit2	0.00785	0.00152	5.15344	0.00000	0.00492	0.01093
PlagYr+YrInit	(Intercept)	6.48033	0.20283	31.94960	0.00000	6.11955	6.86326
PlagYr+YrInit	plagyr	0.02163	0.00825	2.62332	0.00915	0.00487	0.03929
PlagYr+YrInit	yrinit	-0.04400	0.01504	-2.92562	0.00370	-0.06778	-0.02002
PlagYr+YrInit2	(Intercept)	7.17733	0.22065	32.52833	0.00000	6.74728	7.64447
PlagYr+YrInit2	plagyr	0.02592	0.00686	3.77701	0.00019	0.01254	0.03984
PlagYr+YrInit2	yrinit	-0.21511	0.03677	-5.85003	0.00000	-0.28856	-0.14606
PlagYr+YrInit2	yrinit2	0.00716	0.00152	4.70237	0.00000	0.00439	0.01013
PlagYr2+YrInit	(Intercept)	6.32406	0.25246	25.04940	0.00000	5.87324	6.80125
PlagYr2+YrInit	plagyr	0.07037	0.05026	1.40028	0.16247	-0.02206	0.16575
PlagYr2+YrInit	plagyr2	-0.00184	0.00188	-0.97668	0.32952	-0.00539	0.00158
PlagYr2+YrInit	yrinit	-0.03845	0.01590	-2.41928	0.01615	-0.06413	-0.01246
PlagYr2+YrInit2	(Intercept)	7.15285	0.28880	24.76714	0.00000	6.63505	7.70126
PlagYr2+YrInit2	plagyr	0.03262	0.04421	0.73767	0.46130	-0.04679	0.11459
PlagYr2+YrInit2	plagyr2	-0.00026	0.00167	-0.15362	0.87802	-0.00335	0.00273
PlagYr2+YrInit2	yrinit	-0.21333	0.04054	-5.26224	0.00000	-0.28961	-0.14113
PlagYr2+YrInit2	yrinit2	0.00711	0.00161	4.41364	0.00001	0.00430	0.01014

Dyn+YrInit2+4Nests	(Intercept)	7.84772	0.15953	49.19427	0.00000	7.54557	8.16390
Dyn+YrInit2+4Nests	dynext	-0.33082	0.19253	-1.71823	0.08678	-0.69629	0.06544
Dyn+YrInit2+4Nests	dyngrow	0.06988	0.09109	0.76713	0.44361	-0.10933	0.24757
Dyn+YrInit2+4Nests	yrinit	0.01748	0.02395	0.72994	0.46599	-0.03211	0.06607
Dyn+YrInit2+4Nests	yrinit2	-0.00067	0.00097	-0.68948	0.49105	-0.00262	0.00133
Dyn+YrInit2+4Nests	X4nesttown	-2.32498	0.14537	-15.99362	0.00000	-2.62200	-2.03842
PlagYr+YrInit2+4Nests	(Intercept)	7.77990	0.16640	46.75363	0.00000	7.46587	8.11447
PlagYr+YrInit2+4Nests	plagyr	0.00933	0.00426	2.18930	0.02935	0.00119	0.01768
PlagYr+YrInit2+4Nests	yrinit	0.00621	0.02405	0.25803	0.79656	-0.04393	0.05476
PlagYr+YrInit2+4Nests	yrinit2	-0.00015	0.00097	-0.15330	0.87826	-0.00209	0.00186
PlagYr+YrInit2+4Nests	X4nesttown	-2.25359	0.15428	-14.60746	0.00000	-2.57996	-1.94420
Dyn+PlagYr+YrInit	(Intercept)	6.44348	0.28768	22.39836	0.00000	5.97097	6.95708
Dyn+PlagYr+YrInit	dynext	1.00160	0.38902	2.57466	0.01052	0.29212	1.78553
Dyn+PlagYr+YrInit	dyngrow	-0.00419	0.21568	-0.01941	0.98452	-0.40054	0.37821
Dyn+PlagYr+YrInit	plagyr	0.02699	0.01036	2.60426	0.00967	0.00730	0.04690
Dyn+PlagYr+YrInit	yrinit	-0.05195	0.01338	-3.88324	0.00013	-0.07465	-0.02982
Dyn+PlagYr2+YrInit	(Intercept)	5.94630	0.34195	17.38961	0.00000	5.31395	6.57953
Dyn+PlagYr2+YrInit	dynext	1.29984	0.39828	3.26362	0.00123	0.58087	2.08824
Dyn+PlagYr2+YrInit	dyngrow	0.15235	0.20964	0.72674	0.46796	-0.25571	0.56449
Dyn+PlagYr2+YrInit	plagyr	0.13851	0.04807	2.88130	0.00425	0.04561	0.23684
Dyn+PlagYr2+YrInit	plagyr2	-0.00397	0.00170	-2.33492	0.02021	-0.00738	-0.00073
Dyn+PlagYr2+YrInit	yrinit	-0.04045	0.01406	-2.87765	0.00430	-0.06410	-0.01644
Dyn+PlagYr+YrInit2	(Intercept)	7.41617	0.34738	21.34865	0.00000	6.77870	8.10562
Dyn+PlagYr+YrInit2	dynext	0.15728	0.37298	0.42167	0.67357	-0.58329	0.94971
Dyn+PlagYr+YrInit2	dyngrow	-0.31580	0.20943	-1.50791	0.13264	-0.73322	0.08214
Dyn+PlagYr+YrInit2	plagyr	0.01726	0.00965	1.78933	0.07458	-0.00213	0.03656
Dyn+PlagYr+YrInit2	yrinit	-0.21247	0.03865	-5.49761	0.00000	-0.28891	-0.13987
Dyn+PlagYr+YrInit2	yrinit2	0.00696	0.00157	4.42998	0.00001	0.00395	0.01014

Dyn+PlagYr2+YrInit2	(Intercept)	7.41589	0.51473	14.40722	0.00000	6.44390	8.40401
Dyn+PlagYr2+YrInit2	dynext	0.15750	0.44824	0.35138	0.72555	-0.74809	1.10571
Dyn+PlagYr2+YrInit2	dyngrow	-0.31570	0.23363	-1.35124	0.17765	-0.79423	0.15799
Dyn+PlagYr2+YrInit2	plagyr	0.01730	0.05583	0.30991	0.75685	-0.08822	0.12855
Dyn+PlagYr2+YrInit2	plagyr2	0.00000	0.00195	-0.00074	0.99941	-0.00381	0.00362
Dyn+PlagYr2+YrInit2	yrinit	-0.21245	0.04888	-4.34632	0.00002	-0.30537	-0.12250
Dyn+PlagYr2+YrInit2	yrinit2	0.00696	0.00185	3.76145	0.00020	0.00343	0.01067
Dyn+PlagYr+4Nests	(Intercept)	7.49909	0.17330	43.27289	0.00000	7.15759	7.86062
Dyn+PlagYr+4Nests	dynext	0.18403	0.20906	0.88030	0.37940	-0.22278	0.60969
Dyn+PlagYr+4Nests	dyngrow	0.46644	0.11766	3.96440	0.00009	0.21546	0.71269
Dyn+PlagYr+4Nests	plagyr	0.02429	0.00561	4.33186	0.00002	0.01268	0.03589
Dyn+PlagYr+4Nests	X4nesttown	-2.35066	0.13943	-16.85900	0.00000	-2.63453	-2.08369
Dyn+PlagYr+YrInit2+4Nests	(Intercept)	7.29133	0.21865	33.34656	0.00000	6.87990	7.72417
Dyn+PlagYr+YrInit2+4Nests	dynext	0.19829	0.22424	0.88429	0.37726	-0.24179	0.65481
Dyn+PlagYr+YrInit2+4Nests	dyngrow	0.51953	0.12897	4.02828	0.00007	0.25404	0.77705
Dyn+PlagYr+YrInit2+4Nests	plagyr	0.02534	0.00581	4.36542	0.00002	0.01357	0.03704
Dyn+PlagYr+YrInit2+4Nests	yrinit	0.03928	0.02484	1.58109	0.11493	-0.01188	0.08919
Dyn+PlagYr+YrInit2+4Nests	yrinit2	-0.00140	0.00099	-1.41638	0.15772	-0.00337	0.00063
Dyn+PlagYr+YrInit2+4Nests	X4nesttown	-2.41681	0.15113	-15.99155	0.00000	-2.72689	-2.11996

Wet = wet (2005=2007) or dry (2006=2008). SprRain = spring rainfall. Year = 2005, 2006, 2007, or 2008. PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Dyn = current town dynamics (extinct, growing, or stable). Grow = growing or not (extinct=stable). Active = active or not. YrInit = years since town was initiated. YrInit2 = YrInit^2. YrInit3 = YrInit^3. Size = town size. Size2 = Size^2.

APPENDIX 4 – NEST DISTANCE MODELS

Table 4.12. Nest Distance Models: Nest Number. Years since the most recent plague event, time since prairie dog town initiation, and current town dynamics were the best predictors of nest spacing, with or without the binary variable differentiating towns with 4+ nests from those with fewer nests. Ranking of other variables did not change when this variable was added to the top models.

Model	AIC	∆AIC	Wt	Deviance	df	#Par
Dyn+PlagYr+YrInit2+4Nests	4023.82	0.00	1.00	110.30	296	7
PlagYr+YrInit2+4Nests	4042.71	18.89	0.00	118.43	298	5
Dyn+PlagYr+4Nests	4044.77	20.95	0.00	112.57	299	5
Dyn+YrInit2+4Nests	4128.42	104.60	0.00	120.18	302	6
4Nests	4187.69	163.87	0.00	124.82	309	2

PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Dyn = current town dynamics (extinct, growing, or stable). YrInit = years since town was initiated. YrInit2 = YrInit^2. 4Nests = towns with ≥ 4 nests vs. those with fewer.

Table 4.13. Nest Distance Models: Inverse Link. Model rankings in the analysis of nest distance (gamma) did not change significantly when an inverse link function was used in place of a log link function. However, five models failed to converge with the inverse link function, and signs on all coefficients (not shown) were reversed.

Model	AIC	∆AIC	Wt	Deviance	df	#Par
Dyn+PlagYr2+YrInit2	4285.90	0.00	1.00	243.94	296	7
PlagYr2+YrInit2	4311.37	25.47	0.00	265.82	298	5
Dyn+PlagYr2+YrInit	4318.60	32.70	0.00	269.89	297	6
PlagYr+YrInit	4328.72	42.82	0.00	282.75	300	3
PlagYr2+YrInit	4329.34	43.44	0.00	281.62	299	4
Dyn+YrInit2	4382.53	96.62	0.00	256.95	303	5
Dyn+PlagYr	4396.94	111.04	0.00	323.19	300	4
PlagYr2	4397.45	111.55	0.00	325.49	301	3
YrInit3	4416.54	130.63	0.00	284.76	304	4
YrInit2	4419.79	133.88	0.00	289.04	305	3
PlagYr	4423.13	137.23	0.00	351.85	302	2
YrInit	4435.74	149.84	0.00	304.08	306	2
Size2	4566.53	280.63	0.00	370.17	308	3
Dyn	4573.21	287.31	0.00	376.97	308	3
Size	4573.43	287.53	0.00	379.25	309	2
Active	4576.41	290.51	0.00	382.33	309	2
Grow	4587.76	301.86	0.00	394.27	309	2
Year	4592.76	306.86	0.00	395.34	307	4
SprRain	4593.05	307.15	0.00	399.95	309	2
Wet	4595.29	309.39	0.00	402.37	309	2
Y2005+2007	4595.43	309.53	0.00	400.35	308	3
Y2005	4597.99	312.09	0.00	405.31	309	2
PlagYr+YrInit2	did not converge					
Dyn+PlagYr2	did not converge					
Dyn+YrInit	did not converge					
Dyn+PlagYr+YrInit	did not converge					
Dyn+PlagYr+YrInit2	did not converge					

Wet = wet (2005=2007) or dry (2006=2008). SprRain = spring rainfall. Year = 2005, 2006, 2007, or 2008. PlagYr = years since most recent plague event. PlagYr2 = PlagYr^2. Dyn = current town dynamics (extinct, growing, or stable). Grow = growing or not (extinct=stable). Active = active or not. YrInit = years since town was initiated. YrInit2 = YrInit^2. YrInit3 = YrInit^3. Size = town size. Size2 = Size^2.

APPENDIX 5 – MINIMUM ESTIMATES OF OWLETS PER AGE

Table 4.14. Breeding Success per Age and Stage. These four ages are frequently referenced in the burrowing owl literature. Not all studies define fledging in the same way, and other stages may be of interest. The percentage of nests with at least one owlet observed at each age are shown, as well as means (SD) for the number of juveniles per nest and the number per nest for just those nests with at least one owlet reaching this age.

Age	Stage	% Nests	# Juvs per nest	# Juvs per nest (successful)
14 d	emerged from nest	85.85%	3.95 (2.45)	4.60 (2.01)
28 d	using satellite burrows, attempts flight	79.74%	3.14 (2.44)	3.94 (2.08)
35 d	flies fairly well	71.06%	2.56 (2.39)	3.61 (2.06)
42 d	ranging farther from nest	56.59%	1.89 (2.26)	3.35 (2.05)