Winter Ecology of Common Ravens in Southern Wyoming and the Effects of Raven Removal on Greater Sage-Grouse Populations

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WINTER ECOLOGY OF COMMON RAVENS IN SOUTHERN WYOMING
AND THE EFFECTS OF RAVEN REMOVAL ON
GREATER SAGE-GROUSE POPULATIONS

by
Luke W. Peebles

A thesis submitted in partial fulfillment
of the requirements for the degree
of
MASTER OF SCIENCE
in
Wildlife Biology

Approved:

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UTAH STATE UNIVERSITY
Logan, Utah
2016
ABSTRACT

Winter Ecology of Common Ravens in Southern Wyoming and the Effects of Raven Removal on Greater Sage-Grouse Populations

by

Luke W. Peebles, Master of Science
Utah State University, 2016

Major Professor: Dr. Michael R. Conover
Department: Wildland Resources

My research focused on common raven (Corvus corax; hereafter raven) winter ecology and removal, and how raven removal aids Greater sage-grouse (Centrocercus urophasianus; hereafter sage-grouse) populations. Raven winter ecology in the western US has not been described in detail. I researched raven use of landfills for foraging and raven use of anthropogenic structures for roosting, as well as dispersal of ravens in the spring. In all, 22% of radio-marked ravens (n = 73) used landfills during the day, and 68% (n = 73) roosted at anthropogenic roost sites during the evening. Correlations between landfill and roost counts of ravens were stronger (0.4 < r < 0.7) when the distance between these sites was <15 km, and smaller (r < 0.3) when this distance >20 km. In the spring, ravens dispersed, on average, 38 km from landfills where they were caught.

Large congregations of ravens at a few sites in winter may present opportunities to initiate raven population reduction methods to alleviate later problems. I analyzed
raven survival and behavior when USDA/APHIS Wildlife Services (WS) removed ravens using DRC-1339 during winter months. The number of ravens killed annually was 7-34% of the local population. Ravens did not avoid landfills, yet they switched roosts more frequently after an application of the toxicant.

Raven removal improves sage-grouse nest success; however, data were not available to examine how raven removal improves sage-grouse abundance. I analyzed changes in raven density with regard to WS removal, and then related these changes with changes in sage-grouse lek counts the following year. Raven densities decreased by 50% from 2008-2014 where WS conducted removal programs. Sage-grouse lek counts improved in areas where WS lowered raven abundance, in comparison to areas farther away, during the latter half of the study (2013-2015), when WS removal efforts intensified. Thereafter, a 10% decline in raven abundance was associated with a 2% increase in sage-grouse lek counts. Overall, ravens in southern Wyoming used anthropogenic resources during the winter, and removal of ravens at these locations, combined with removal in the spring, minimally impacted raven populations annually and was associated with increases in sage-grouse abundance.

(137 pages)
PUBLIC ABSTRACT

Winter Ecology of Common Ravens in Southern Wyoming and the Effects of Raven Removal on Greater Sage-Grouse Populations

by

Luke W. Peebles

Common raven (Corvus corax; hereafter raven) populations have been increasing rapidly in the western United States, and these ravens cause damage to livestock, human health and safety, and wildlife species including greater sage-grouse (Centrocercus urophasianus; hereafter sage-grouse). The goals of my research were to gain a better understanding of the winter ecology of ravens, to see how raven populations were impacted by intensive removal during the winter, and to determine if raven removal aids sage-grouse populations. I found that ravens captured at landfills used these landfills sporadically for foraging, and these ravens regularly used bridges and industrial sites for roosting in the evening. Raven counts at anthropogenic roost sites and landfills fluctuated similarly when these locations were <15 km away from each other. In the spring, ravens dispersed, on average, 38 km from landfills where they were caught.

Raven removal applied during the winter may alleviate damage caused by ravens in the spring and summer months. I analyzed raven survival and behavior when USDA/APHIS Wildlife Services (WS) removed ravens using DRC-1339. I found that 7-34% of the raven population was removed annually from these efforts. Ravens did not avoid landfills after poisoning, but ravens switched roosts after a DRC-1339 application.
Recent studies have indicated that raven removal improves sage-grouse nest success. However, connections between raven removal and sage-grouse abundance have not been explored in detail. I analyzed changes in raven density with regard to WS removal, and then related changes in landscape raven density with changes in sage-grouse lek counts the following year. Raven densities decreased by 50% from 2008-2014 where WS removed ravens. Sage-grouse lek counts did not improve in areas where WS lowered the abundance of ravens, in comparison to areas farther away, until the latter half of the study (2013-2015) when raven removal increased. Thereafter, a 10% decline in raven numbers increased sage-grouse numbers by 2%. 
ACKNOWLEDGMENTS

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Luke W. Peebles
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CHAPTER 1
INTRODUCTION AND LITERATURE REVIEW

An increase in common raven (Corvus corax; hereafter raven) numbers across the western United States has been linked to expanding human activity (Leu et al. 2008). In the last few decades, raven populations have increased from 300% to >1500% in certain areas (Knight et al. 1993, Saur et al. 2011). Prime foraging and breeding habitat for ravens have been created as the result of human activity. For example, landfills are an important food resource for ravens in the wintertime, and landfills can allow raven abundance to increase (Restani et al. 2001, Preston 2005). Vehicular traffic also provides ravens access to road-killed animals throughout the winter (Boarman and Heinrich 1999).

Nests are often located in industrial plant towers, power poles, and other elevated anthropogenic structures (Knight and Kawashima 1993, Steenhof et al. 1993). Anthropogenic structures are also important sites for raven roosts; large numbers of ravens have been observed roosting on transmission lines and at industrial sites (Engel et al. 1992, Boarman et al. 1995, Merrell 2012). Human altered areas have 2 major effects; they increase raven chick production and survival, and they draw in ravens from surrounding areas (Kristen et al. 2004, Webb et al. 2004, Fleisher et al. 2008).

Ravens cause numerous problems. They depredate young livestock (Larsen and Dietrich 1970, Spencer 2002) and pose human health and safety concerns. Ravens deposit fecal matter in high quantities in areas when they roost and nest, creating a health hazard to employees at industrial sites (Engel et al. 1992, Merrell 2012). Nesting ravens can become aggressive towards industry employees that approach nests that are
established around buildings and other work structures (Merrell 2012). Raven also prey upon eggs and young of wildlife species, including the desert tortoise (*Gopherus agassizii*), California least tern (*Sterna antillarum browni*), and Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse; Linz et al. 1990, Boarman 2003, Coates et al. 2008).

Raven management in the western US has been tailored to solve problems as they arise; most raven removal occurs in the spring and summer months, which coincides with calving, lambing, and the breeding activities of affected wildlife species. Thus, raven ecology studies in the western US are often conducted during this time. Studies have included analyses of diet (Kristen et al. 2004), habitat use (Boarman et al. 1995, Coates et al. 2014), and movements (Linz et al. 1992, Roth et al. 2004). In contrast, little is known about the winter ecology of ravens in the western US. A few studies have indicated that landfills are important food resources for ravens in western North America. Lack of food elsewhere during snowfall and low temperatures increases raven use of landfills (Dorn 1972, Preston 2005). Ravens in the western US often roost in anthropogenic structures in winter, rather than trees (Lucid and Conner 1974, Engel et al. 1992b, Marzluff et al. 1996, Wright et al. 2003, Merrell 2012). Relationships between food resources and roost locations in the eastern US during winter are well documented; ravens use roosts as mobile information centers to communicate the location of food that is sporadically distributed (Marzluff et al. 1996, Wright et al. 2003). In western North America, connections between roost locations and landfills during the winter have not been described in detail. Also, little is known about how far ravens disperse from areas of winter congregation. Ravens are highly vagrant. Heinrich et al. (1994) found that 90%
of radio-marked ravens captured within a 5,000 km² area in February left by mid-March. This movement coincides with increases in alternative food resources and when breeding ravens start nesting (Boarman and Heinrich 1999). Ravens often disperse >100 km during the spring and summer outside of North America (Skarphédinsson et al. 1990, Restani et al. 2001).

Raven management in the winter may be a viable option to reduce problems that occur later. Raven control is conducted by distributing 3-chloro-p-toluidine hydrochloride (DRC-1339), a toxicant that is very selective. Ravens are highly susceptible to it, but it is comparatively innocuous to other avian and mammalian species (Decino et al. 1966). This toxin is often injected into chicken eggs or sprayed on meat cubes and dog food. Treated baits are then distributed where they will be consumed by ravens, often after a pre-baiting program so that ravens get used to consuming the bait. DRC-1339 is slow-acting, causing death 3-50 hours after ingestion because of kidney necrosis (Decino et al. 1966). Other than toxicants, shooting is the only other viable option for removal. However, shooting is only effective for removal of single ravens or pairs of ravens because flocks of ravens learn quickly how to avoid shooting (Merrell 2012).

Removal efforts using DRC-1339 and other methods often result in short-term reductions in raven populations at treatment sites; however, raven removal varies in long-term effectiveness. Larsen and Dietrich (1970) reduced a raven population of 200 ravens by 90% in a 3-week baiting period. They found only 10 ravens (5% of the original population) at the treatment site the year following application. In Nevada, DRC-1339 treated areas resulted in raven density reductions to near zero. However, raven numbers
returned to pre-treatment levels in Nevada 1 year after treatment (Coates et al. 2007). An intensive removal program in Iceland removed an average of 4,116 common ravens annually from 1981-1985; the number of breeding pairs did not fluctuate significantly during this time period, but a decline in the non-breeding population was observed (Skarphéðinsson et al. 1990).

The long delay between ingestion of DRC-1339 and death makes it difficult to determine how many ravens are killed during an application of the toxicant. Techniques used to monitor raven mortality after an application of DRC-1339 vary considerably. One method involves using bait consumption. Coates et al. (2007) estimated raven mortality from baiting by calculating that 1 raven died for every 11 poisoned eggs that disappeared or were eaten. Another method involves retrieving raven carcasses. Butchko (1990) conducted extensive searches in the landfill where eggs treated with DRC-1339 were distributed and retrieved 78 raven carcasses; he used this number, combined with the number of shot ravens, to calculate the mortality rate. Counts of live ravens are also used to estimate raven mortality; Larsen and Dietrich (1970) did not report finding raven carcasses after using DCR-1339, only that ravens were absent at lambing grounds. However, the presence of dead or dying ravens after a DRC-1339 application may deter ravens from returning to baited areas so counting ravens at areas of DRC-1339 application may overestimate the number of ravens killed (Merrell 2012, Peterson and Colwell 2014).

Raven removal has been considered a viable option for helping wildlife populations in peril. One such species is the sage-grouse. In contrast to raven populations, sage-grouse populations have experienced significant population declines
across western North America. Sage-grouse were traditionally found in 16 states in the U.S. and 3 Canadian provinces (Patterson 1952). Currently, sage-grouse occupy 56% of their historical range prior to European settlement (Schroeder et al. 2004). The major contributing factor to the long-term decline of sage-grouse is the loss of suitable habitat containing sagebrush (*Artemesia* spp.). Sagebrush habitat has declined by 2.5 million ha since the turn of the 20th century (Braun 1998, Schroeder et al. 1999).

Large-scale habitat degradation, along with the encroachment of humans, can have numerous secondary consequences, including increased vulnerability to predation. Nest predation in fragmented sagebrush habitat has the potential to reduce sage-grouse productivity, which in turn, can subsequently affect the sustainability of sage-grouse populations (Gregg et al. 1994, Braun 1998). Ravens are significant predators of sage-grouse eggs and chicks. Nest depredation rates range anywhere from 10% to 50% (Allred 1942, Batterson and Morse 1948, Coates et al. 2008). Ravens, as generalist predators, do not have to rely on sage-grouse as their sole food-source. The abundance of generalist predators is not linked to the abundance of a particular species (Schroeder and Baydack 2001, Coates 2007). Even if prey populations are low in number, generalist predators can continue to depredate bird nests at high rates because the generalist can augment prey from many species (Vickery et al. 1992, Boarman 1993, Sinclair et al. 1998).

Because of threats to declining sage-grouse populations, raven control has been tested to determine whether sage-grouse nest success is improved by reducing raven abundance. In Oregon, Batterson and Morse (1948) experimentally removed ravens for the benefit of sage-grouse. They reported a 51% nest success rate in the treatment area.
and a 6% nest success rate in a non-treated area. In Nevada, Coates et al. (2007) found that raven densities dropped to near zero every year after DRC-1339 applications. They found that an increase of 1 raven per 10 km of transect increased the odds of sage-grouse nest failure by 7.4% (Coates and Delehanty 2010). In southwestern Wyoming, raven densities declined in raven removal study sites where WS applied DRC-1339 and increased in non-removal study sites (Dinkins 2013). Sage-grouse nest success was 22% where ravens were spotted within 550 m of a nest and 41% where ravens were absent. These results suggest that raven removal can improve nesting success of sage-grouse. However, none of these studies addressed the effects of raven removal on sage-grouse populations. It is suspected that long-term benefits of raven removal for sage-grouse are minimal (Coates 2007, Bui et al. 2010, Hagen 2011). In general, corvid removal has been found to increase productivity of bird species but have minimal effects on bird abundance (Côté and Sutherland 1997, Madden et al. 2015).

**RESEARCH OBJECTIVES**

My objectives were to 1) describe and explain raven ecology and spring dispersal of ravens 2) determine how raven winter removal programs affected the raven population and 3) determine how raven abundance within sage-grouse nesting habitat affected sage-grouse abundance.

Raven ecology in the winter has not been thoroughly examined in the western US, but studies of the ecology of wintering ravens may shed light on preventative raven management that could alleviate subsequent raven damage. In Chapter 2, I examined raven use of landfills for foraging and the use of anthropogenic structures for roosting during the winter. I then looked at count data between specific landfill-roost pairs and
determined connectivity between pairs. I tested environmental variables (day length, lunar cycle, precipitation, and temperature) to explain the relationships observed in the count data at roosts and landfills. Lastly, I used radio-marked ravens to investigate raven dispersal from winter congregation areas to spring locations to determine the distance ravens traveled to spring foraging and nesting locations.

Raven management has been conducted by USDA/APHIS, Wildlife Services (WS) in southern Wyoming for the protection of livestock and human health. DRC-1339 is the preferred toxicant for most raven removal in the area. In recent years (2013-2015), emphasis has been placed on removing ravens in winter to prevent problems from occurring. This change in tactics provided an opportunity to access raven control outside of corrective control, which is applied on-site to offending ravens. In Chapter 3, I monitored winter raven survival and changes in raven population numbers from 2013-2015. I hypothesized that there would be short-term reductions in the raven population in southwest Wyoming after the use of DRC-1339 to remove ravens, and that raven population estimates the following winter would be minimally affected by WS removal conducted the previous winter. Another goal was to determine if ravens learned to avoid landfills and roosts where DRC-1339 was applied. I hypothesized that ravens, with their high level of intelligence, would learn to avoid areas of application. I also tested 3 methods to estimate raven mortality to determine which one(s) provided the best estimates without the use of radio-telemetry. Methods included carcass counts, counts at landfills and other treatment areas, and roost counts.

Reduction of raven densities in areas of sage-grouse occupancy needs to be analyzed over the long-term to determine if decreased depredation risk by ravens
improves sage-grouse populations. Raven removal has been conducted by WS in southern Wyoming from 2007–2015 for the protection of livestock and human health. This raven removal provided an opportunity to study the potential effects of raven removal on sage-grouse population dynamics. In Chapter 4, I hypothesized that sage-grouse lek counts would increase in areas where WS lowered raven densities. To test this hypothesis, I compared changes in raven densities and sage-grouse lek counts from 2008-2015 in areas within proximity of WS raven removal and in areas farther away.

The chapters of my thesis are organized and written as separate manuscripts. Chapters 1 is in the format of the Journal of Wildlife Management. Chapters 2-4 are in the format of the Wildlife Society Bulletin. Chapters 5 is in the format of the Journal of Wildlife Management.

LITERATURE CITED


Coates, P. S., K. B. Howe, M. L. Casazza, and D. J. Delehanty. 2014. Landscape alterations influence differential habitat use of nesting buteos and ravens within


CHAPTER 2

WINTER ECOLOGY AND SPRING DISPERsal OF COMMON RAVENS IN WYOMING

ABSTRACT Populations of common ravens (*Corvus corax*) have increased in western North America and cause problems throughout their range. However, little is known about their winter ecology. I studied a raven population in Wyoming from 2013-2015; my goals were to examine raven use of landfills for foraging and anthropogenic structures for roosting during winter, as well as dispersal patterns of ravens from these landfills in the spring. On average, 22% of radio-marked ravens (*n* = 73) foraged at landfills on a given day, and 68% of these ravens roosted at documented anthropogenic sites (e.g. buildings or underneath bridges) each night. Anthropogenic roost and landfill count correlations were highest (*0.4 < r < 0.7*) between the closest roost-landfill pairs (*n* = 12). Correlation between landfill and roost counts may be largely driven by distance between these 2 sites, with connectivity declining as distance increased >20 km. Increased precipitation and decreased temperatures increased raven use of landfills and anthropogenic roost sites. In the spring, radio-marked ravens (*n* = 56) dispersed, on average, 38 km from landfills where they were captured. High site fidelity to landfills and anthropogenic roost sites in the winter likely contributes to an increase in the raven population by improving raven survival and body condition of breeding-aged birds. Most ravens moved <40 km from these locations in the spring. Therefore, areas susceptible to raven damage were localized within a 40 km radius of where ravens wintered.
INTRODUCTION

Common raven (*Corvus corax*; hereafter raven) populations have increased several fold in the western U.S. during the last several decades (Boarman 1993, Boarman and Berry 1995, Sauer et al. 2011). These ravens pose health and safety hazards to humans by roosting and defecating in areas used by humans (Engel et al. 1992a, Merrell 2012). Ravens also kill young livestock (Larsen and Dietrich 1970, Spencer 2002) and wildlife species including the desert tortoise (*Gopherus agassizii*), California least tern (*Sterna antillarum browni*), and Greater sage-grouse (*Centrocercus urophasianus*; Linz et al. 1990, Boarman 2003, Coates et al. 2008). Most studies on raven ecology occur during the spring and summer when ravens cause problems. In contrast, little research has been focused on the winter ecology of ravens in the western U.S. What is known about the winter ecology of ravens in the western U.S. suggests that it is different than the winter ecology of ravens in the eastern U.S. Ravens in the western U.S. utilize landfills heavily in winter (Dorn 1972, Preston 2005), whereas exposed carcasses are the main winter food source of ravens in the eastern U.S. (Heinrich 1988, Marzluff et al. 1996, Wright et al. 2003). Ravens often roost in anthropogenic structures in the western U.S., rather than trees and natural substrate (Brown 1974, Lucid and Conner 1974, Temple 1974, Engel et al. 1992b, Cotterman and Heinrich 1993, Marzluff et al. 1996, Wright et al. 2003, Merrell 2012).

Ravens in eastern North America are highly vagrant when spring approaches. Heinrich et al. (1994) found that only 1 of 10 radio-marked ravens captured in February were present in a 5,000 km² area by mid-March when breeding pairs of ravens establish
nests (Boarman and Heinrich 1999). In western North America, raven dispersal from areas of winter congregation has not been described.

In Wyoming, ravens congregate in large numbers during the winter at landfills and at roosts located within anthropogenic structures. To determine raven fidelity at landfills and anthropogenic roost sites, I examined weekly and daily use of these locations by ravens. I then compared raven count data between specific landfill-roost pairs and determined connectivity between pairs. I tested environmental variables (e.g., day length, lunar cycle, precipitation, and temperature) to explain the variation in numbers of ravens using landfills and anthropogenic roost sites. Finally, I looked at raven dispersal from landfills to spring locations to see how far ravens traveled.

STUDY AREA

I monitored raven activity at 3 landfills and 5 large (\(\bar{x} >150\) ravens) roosts in Lincoln and Sweetwater counties, in southwest Wyoming, during the winter months (1 November – 31 March) from 2013-2015 (Fig. 2-1). The Kemmerer landfill was monitored all 3 years, and it was where most ravens were captured for radio-marking. Garbage at this landfill was packaged into large bales, stacked in an open pit, and covered with approximately 15 cm of dirt most days. However, the sides of the newest rows of bales were left exposed and available for raven foraging. I also captured ravens at the Green River and Rock Springs landfills and monitored them for raven activity after the discovery of radio-marked ravens at these locations in November 2014 and January 2015, respectively. Both of these landfills utilized a “loose-fill” approach: garbage was dumped into an open pit, crushed with a compactor, and covered with approximately 15 cm of dirt 2 to 3 times a week.
My study area in rural Wyoming lacked large groves of trees suitable for roosting in the winter months. Instead, ravens roosted at industrial sites or under bridges. From the winters of 2013-2015, I monitored 5 raven roosts, all within 30 km of the nearest landfill. Roost sites were all man-made, including railroad bridges and industrial sites. Roost sites differed from year to year.

The study area encompassed approximately 5,000 km², and the elevation was, on average, 2,100 m. The habitat surrounding the landfills was largely composed of sagebrush (*Artemisia* spp.) plant communities. Agricultural use was limited to mainly cattle and sheep grazing across the study area; most land was managed for multiple-use by the Bureau of Land Management (BLM). Oil and gas sequestration composed the highest land use activity outside of agriculture. During the winter months from 2013-2015, Kemmerer received an average of 6 cm of precipitation, and daily temperatures averaged -4 °C. Green River and Rock Springs received 7 cm of precipitation from November 2014 to March 2015; daily temperatures averaged -0.1 °C.

**METHODS**

I captured ravens using #3 leg-hold traps (Oneida Victor® Soft Catch® Coil, Euclid, Ohio) placed within landfills and near road-kills or carcasses. Captured ravens were equipped with either 19- or 24-g VHF backpack transmitters (Model A1135/A1140, Advanced Telemetry Systems, Insanti, Minnesota) or 30-g solar-powered GPS PTT transmitters (North Star Science and Technology, King George, Virginia). All ravens were released at their capture site as soon as the transmitters were attached. These methods were approved by the Institutional Animal Care and Use Committee of Utah.
State University (Protocol number 2031), the U.S. Fish and Wildlife Service (banding permit #21175), and the Wyoming Game and Fish Department (Chapter 33 Permit #657).

Landfills used by radio-marked ravens were easy to locate, and ravens consistently used these locations during the study. However, roosting locations changed annually and were harder to find. To locate raven roosts, I examined numerous bridges and chemical plants for radio-marked ravens, questioned plant personnel and local residents, used night-surveys (visual and audio), and looked for whitewash (areas of large amounts of raven fecal matter).

Stationary data loggers (Model 4500S, Advanced Telemetry Systems, Insanti, Minnesota) equipped with 3-element Yagi antennae (Communications Specialists, Orange, California) recorded telemetry data for radio-marked ravens at landfills and documented anthropogenic roost sites on a continual basis throughout the winter months. Data loggers picked up radio-marked ravens 1 km from where they were positioned based on field testing and cross-testing with hand-held receivers. I programmed the data-loggers to detect transmitter frequencies and store them for subsequent downloading. I also utilized Communications Specialists (Communications Specialists, R-1000, Orange, California) receivers and 3-element Yagi antennae at landfills (throughout the day) and at anthropogenic roost sites (once each night after all roosting ravens were present) where data loggers were not stationed.

Ravens equipped with the GPS transmitters were monitored on a daily basis using data collected from Argos satellites. Six points per raven per day were collected at 0000, 0700, 1000, 1300, 1600, and 1900 Mountain Standard Time. Most days (98%) contained
≥1 GPS location fix for each raven equipped with a GPS transmitter. Solar charging issues (e.g., feathers covering the solar cell) contributed to most lost fixes (2%).

I counted ravens at the Kemmerer, Green River, and Rock Springs landfills multiple times per week to assess changes in raven numbers across time and between sites. Counts were conducted every 15 min, and most surveys lasted from dawn until 1-2 hrs before dark. Counts were conducted at a pre-determined, elevated location within each landfill that provided the best view of the garbage where ravens were foraging. I determined the number of different ravens using a landfill during a day by determining the maximum number of ravens at the landfill during a particular day. This maximum count, however, needed to be adjusted to account for ravens that used the landfill that day but were not there at the time of the maximum number. I did so by noting how many of the radio-marked ravens were present at the time of the maximum raven count and how many visited the landfill that day, regardless of when they were there. I then divided the maximum raven count by the detection probability, which is the proportion of radio-marked ravens at the landfill during the maximum count, to estimate the total number of ravens at the landfill that day. Evening roost counts were conducted multiple times per week at the 5 roosts (Viaduct, Port of Entry, Encana, Solvay Chemicals, and Shute Creek). Surveys consisted of counting individual ravens as they entered the roost or associated staging areas. Counts began 1-2 hrs before dusk, before most ravens arrived, and continued until darkness prevented further counting.

I analyzed raven use of landfills and anthropogenic structures for roosting over time to determine fidelity at each site. I monitored radio-marked ravens weekly and recorded whether they were present or absent from the roost or landfill they used the
prior week. I also calculated the percentage of radio-marked ravens known to be alive and transmitting signals that used landfills and anthropogenic roost sites on a daily basis. These percentages were calculated on days and nights when all landfills and known roost sites were monitored for radio-marked ravens. To examine connectivity of raven use of landfills and anthropogenic roost sites, I looked at the number of ravens attending landfills and anthropogenic roost sites to see if changes were parallel (i.e. landfill attendance and anthropogenic roost attendance increased and declined similarly) or random (i.e., no patterns were apparent). I analyzed these data using a Poisson regression for each landfill-roost pair. Poisson regression is appropriate for count data that do not have values <0. Poisson regressions were conducted using generalized linear models (GLMs) in R, version 3.2.2. I measured goodness-of fit by using an $r^2$-squared term from Cameron and Windmeijer (1996):

$$R^2 = 1 - \frac{\text{Deviance}}{\text{Deviance}_{\text{null}}}$$

Deviance refers to a quality of fit statistic for a model. The correlation coefficient ($r$) from the $r^2$-squared term was compared across the same landfill paired with different anthropogenic roosts, and visa-versa. Higher $r$ values suggest higher connectivity between the landfill-roost pair. Roost count data were scant in the 2012-2013 winter. Therefore, roost-landfill correlations were only measured during the winters of 2013-2014 and 2014-2015.

Ravens often forage in the hours before and after roosting (Engel and Young 1989). To examine how raven landfill attendance changes throughout the day, I grouped the number of radio-marked ravens present at the landfill hourly and recorded the total number of radio-marked ravens that visited each landfill daily. I then used these data to
compare the percentages of radio-marked ravens, out of the total number of radio-marked ravens that visited the landfill during every hour of the day. I compared these data with count data at the landfill by averaging 4 15-min counts for each hour and recording the average number of ravens per hour utilizing the landfill. Each landfill’s data were recorded separately. Data were available from November-March for the Kemmerer and Green River landfills, whereas data were available from January-March for the Rock Springs landfill.

From January-March 2015, I included behavior data at each 15-min landfill count. I classified each individual raven activity into 3 categories: foraging, loafing, and flying. I focused most of our attention on foraging behavior; this was the primary behavior of interest. Ravens were considered to be foraging if they were seen swallowing garbage, inserting their bills into garbage, or competing for food with conspecifics. Loafing behavior included resting postures, such as perching, as well as maintenance behaviors, such as preening. Individuals were considered as flying any time that the bird was airborne. I recorded the numbers of ravens foraging at each landfill count, and we divided the number of ravens foraging by the total number of ravens at each landfill count to determine the percentages of ravens in the landfill foraging at each 15-min time step. I then grouped foraging behavior data hourly, similar to the landfill count data, to compare raven behavior to hourly raven landfill attendance. Each landfill’s behavior data were recorded separately. A Kruskal-Wallis test was used to detect differences in raven foraging behavior across all landfills. Pairwise comparisons of raven foraging behavior between different landfills were made using the “posthoc.kruskal.nemenyi.test” function in the “PMCMR” package, version 1.2, in R.
Environmental conditions may explain variation in the daily numbers of ravens using anthropogenic roost sites and landfills. I obtained daily lunar cycle and day length data from the Astronomical Applications Department of the United States Naval Observatory (USNO, Washington, DC). Lunar cycle data (moonlight) were recorded as the fraction of the moon illuminated at midnight, Mountain Standard Time, without regard to cloud cover. Day length data were recorded as the total time that any portion of the sun was above the horizon. Day length data for the project were extracted from the city closest to each anthropogenic roost site and landfill.

I obtained daily climate data from National Oceanic and Atmospheric Administration (NOAA) weather stations located within the vicinity (<10 km) of landfills and anthropogenic roost sites. Data obtained from these stations included daily maximum temperature (Tmax; °C), daily minimum temperature (Tmin; °C), and daily precipitation (cm), which was usually snow. Maximum temperatures were applied to the landfill data because they better represent the daytime temperatures when ravens are foraging. The minimum daily temperatures, in contrast, were applied to the roost data because they better represent nocturnal temperatures. Precipitation was modeled for landfill and roost data as a quantitative variable and a categorical variable (no precipitation = “0”, precipitation = “1”) because precipitation in the study area was sporadic; 14% of roost nights and 22% of foraging days had precipitation. I used Akaike’s information criterion corrected for small sample sizes (AICc) to determine the more appropriate measure of precipitation for each dataset.

I analyzed environmental effects on the numbers of ravens attending anthropogenic roosts and landfills using Poisson GLMs in R. Models were compared
with AICc and Akaike weights ($w_i$; Burnham and Anderson 2002) using the “aictab” function, package “bbmle,” version 1.0.17 in R. I used model averaging over a cumulative AICc weight of 90% when large numbers of models were competitive (<4 AICc) and/or if model weights were widely distributed, and thus contained high amounts of uncertainty (Arnold 2010). I performed model averaging using the “model.avg” function in the “MuMIn” package, R version 1.10.5. Before analyzing groups of covariates, I used a Pearson’s correlation matrix to identify multicollinearity between pairs of variables. If $r \geq 0.65$, the pair of variables were not included in the same model.

Fixed-wing telemetry flights were conducted in the spring to locate radio-marked ravens and calculate the distance from winter roost sites. I gridded an area covering approximately 23,000 km$^2$ centered on Kemmerer, WY, which was where most ravens were captured. The aircraft was equipped with 2 3-element Yagi antennae mounted on the wing struts to increase detection probability, and a hand-held receiver was used to locate signals transmitted from ravens. Each VHF-marked raven was located once. Most flights were conducted from 15 May to 31 May. However, 1 flight took place the last week in April of 2014. Locations from GPS-marked ravens were obtained in a similar fashion. However, because these transmitters record data at specific time intervals, they were reported separately from the VHF-marked sample. GPS locations in April and May were analyzed to compare with VHF raven data.

RESULTS

Twenty-three ravens were captured and radio-marked from January-March 2013; 25 from November 2013-February 2014. Seven ravens radio-marked during 2013 were still alive, transmitting a signal, and in the area during the winter of 2013-2014; thus, my
sample size was 32 ravens. Twenty-five ravens were captured from November 2014-February 2015. Nine previously radio-marked ravens were still alive, transmitting a signal, and in the area during the winter of 2014-2015; thus, my sample size was 34 ravens.

Extensive effort yielded the location of 5 large (≥150 ravens) roost sites during the winters of 2013-2015. During the winter of 2013, a 125-m long viaduct in Kemmerer was used as a roost by ravens (hereafter “Viaduct roost”), but a year later ravens abandoned this roost and moved to a 70-m long railroad bridge next to the Kemmerer Port of Entry (hereafter “Port of Entry roost”). At both structures, ravens roosted below the road deck pavement on metal I-beams, which provided overhead and horizontal protection. In the winter of 2015, most ravens left the Port of Entry roost and roosted at an abandoned molten sulfur-loading terminal owned by Encana (hereafter “Encana roost”). The predominant roosting structures at the Encana roost were the concrete storage tanks, metal I-beams, and the metal overhead walkway, and these structures had horizontal protection, limited overhead protection, and were not enclosed. Radio-marked ravens at the Port of Entry roost and the Encana roost were constantly switching between these 2 locations, and these roosts were closer together than any other pair of roosts in the study; they were separated by 12 km, whereas the rest of the roosts were separated by 40 to 80 km. Therefore, I considered these 2 roosts as a single, combined roost (hereafter “Port of Entry/Encana roost”). We monitored 2 other roosts from 2013-2015: the Shute Creek natural gas plant (hereafter “Shute Creek roost”) and the Solvay Chemicals soda ash plant (hereafter “Solvay Chemicals roost”). At these industrial sites, ravens roosted mainly on pipe racks where heated gas was being piped in the facilities.
The likelihood of observing a radio-marked raven at a landfill or anthropogenic roost site it used a week earlier was 70% and 84%, respectively. During the day, 22% (SE = 1%) of the radio-marked sample of ravens, on average, were present at landfills. During the evening, 68% (SE = 1%) of the radio-marked sample of ravens, on average, were found at anthropogenic roost sites under surveillance. I analyzed 264 concurrent roost and landfill counts. Correlation coefficients of count data between specific roost and landfill pairs ranged between $r = 0.06$ and $r = 0.62$. Correlations were highest between the closest roost-landfill pairs, and correlations declined significantly as that distance increased (Table 2-1; Figs. 2-2–2-5). Radio-marked ravens tended to use the anthropogenic roost site closest to the landfill where they were foraging (Table 2-2).

I conducted 5,004 15-min counts at landfills and recorded 4,620 hours of radiotelemetry data at landfills from November-March of 2013-2015. Numbers of ravens fluctuated greatly on an hourly basis. Raven numbers and the percentage of radio-marked ravens at 1 landfill increased until mid-morning, then remained relatively constant until another increase in the latter hours of the day (Figs. 2-6 and 2-7). Raven numbers at the other 2 landfills were highest in the morning, and attendance dropped substantially afterwards; similar patterns were observed in the hourly percentages of radio-marked ravens at these locations (Figs. 2-6 and 2-7).

I recorded behavioral observations of ravens over 2,349 15-minute landfill counts from January-March 2015. Loafing ($\bar{x} = 54\%$) was the dominant behavior at landfills, followed by foraging ($\bar{x} = 28\%$) and flying ($\bar{x} = 18\%$). The percentages of ravens foraging were significantly different across sites ($\chi^2 = 198.67, P < 0.01$). Post-hoc comparisons revealed that the Kemmerer landfill had the most foraging ($\bar{x} =$
36%) compared to the Green River (\(\bar{x} = 11\%\)) and Rock Springs landfills (\(\bar{x} = 24\%;\ Ps < 0.01\); Fig. 2-8).

Hourly comparisons of foraging behavior show different behavioral trends among landfills. At all landfills, ravens spent the most time foraging within a few hours after they arrived (Fig. 2-8). The average percentages of ravens foraging varied significantly among landfills later in the morning and in the afternoon; the Kemmerer landfill remained constant in the amount of foraging observed, the Green River landfill saw rapid declines in foraging, and the Rock Springs landfill saw declines in foraging mid-day, with a substantial increase in foraging at the end of the day (Fig. 2-8).

I analyzed the effects of environmental variables on raven numbers at landfills for 130 landfill days. With regard to the landfill attendance model, the qualitative precipitation model had an AIC\(_c\) score that was >4 with regard to the quantitative precipitation model, so we used the former for further analysis (Burnham and Anderson 2002). When all variables were considered, the top model was >4 \(\Delta\)AIC\(_c\) from the other 14 environmental models considered (Table 2-3); for simplicity, I will discuss the top model. Temperature had negative effects on numbers of ravens attending landfills (Table 2-4); an increase in 1°C of temperature resulted in a 6% (95% CI = 5-7%) decrease in ravens using landfills. Moonlight and precipitation had positive effects on numbers of ravens attending landfills (Table 2-4); a 10% increase in moonlight resulted in 37% (95% CI = 3-79%) more ravens utilizing landfills, whereas the presence of precipitation resulted in a 34% (95% CI = 8-69%) increase in the numbers of ravens utilizing landfills. Day length was not an informative predictor of the number of ravens utilizing landfills (Table 2-4).
I analyzed the effects of environmental variables on raven numbers at anthropogenic roost sites for 241 roost nights. The qualitative precipitation model for roost attendance had an AIC$_c$ score that was >4 with regard to the quantitative precipitation model, so we used the former for further analysis (Burnham and Anderson 2002). Two models out of the 15 environmental models considered were highly competitive with each other (Table 2-5). The top 2 AIC$_c$ selected models contained 90% of the model weight; therefore, I employed model averaging. Minimum temperature had negative effects on numbers of ravens roosting at anthropogenic structures (Table 2-6); a decrease of 1°C in temperature resulted in a 2% (95% CI = 1-3%) increase in the number of ravens roosting at these locations. Moonlight and day length were uninformative predictors of roost size at anthropogenic structures (Table 2-6). Precipitation was an imprecise predictor of roost size; the presence of precipitation resulted in a 13% increase (95% CI = -5% to 30%) in the number of ravens roosting at a documented anthropogenic roost site. However, it did contribute to describing the data (Table 2-6).

I obtained 51 spring dispersal locations of VHF-marked ravens from 2013-2015 (Fig. 2-9). VHF-marked ravens dispersed, on average, 38 km (SE = 4 km) from landfills where they were captured and spent the winter. Most ravens (75%) dispersed within 50 km of their capture locations. The longest dispersal distance recorded for a VHF-marked raven was 98 km. I obtained 1,383 locations from 5 GPS-marked ravens during the spring (Fig. 2-10). GPS-marked raven locations were 39 km (SE = 1 km), on average, away from the landfills where they were captured. Most GPS locations (75%) were within 60 km of the landfills where they were captured. The furthest recorded distance, from the point of capture, for a GPS-marked raven was 151 km.
DISCUSSION

Ravens regularly visited landfills they attended the week before; however, only 22% of the radio-marked sample were found at landfills on any given day. Other foraging sites including paved highways, towns, and abundant livestock operations in the study site provided adequate food resources for ravens. I opportunistically observed radio-marked ravens feeding at ungulate carcasses, livestock feed lines, and livestock carcasses, with some ravens foraging >40 km away from landfills and roosts. Several studies have shown that small mammals and the remains of larger mammals represent larger proportions of food items in raven diets than garbage (Temple 1974, Harlow et al. 1975, Engel and Young 1989, Kristen et al. 2004). Ravens regularly visited anthropogenic roost sites they attended the week before, and 68% of the radio-marked sample were found at these sites nightly. This may be reflective of the low availability of alternate roosting substrate. Elsewhere in North America, large raven roosts (>100 ravens) have been found in natural substrate, such as trees and cliffs (Cushing 1941, Temple 1974, Lucid and Conner 1974, Heinrich 1988). In my study area, which is predominantly sagebrush, large stands of trees and cliffs suitable for roosting are distant from major food sources. Therefore, bridges and industrial sites represent the most suitable roosting structures for large numbers of ravens during the winter. In my study area, ravens did not utilize coniferous trees in towns for roosting, which are popular roost locations for similar corvids like American crows (Corvus brachyrhynchos; Kalmbach 1915, Emlen 1938, Gorenzel and Salmon 1995), perhaps because the stands of trees were too small to accommodate hundreds of ravens. Coniferous tree stands had <5 trees per stand, and Marzluff et al. (1996) reported ravens utilizing dense groves of conifers.
Landfill use by ravens was often connected to raven use of anthropogenic structures for roosting in southwest Wyoming. Correlations between roost-landfill pairs were higher (0.40 < r < 0.70) when the distance between the two locations was <15 km. Distance from roosts seems to be a determining factor in landfill use by ravens that roost at anthropogenic structures, or visa-versa; the 2 landfills that were >20 km from their closest anthropogenic roost site saw significantly less foraging than the landfill that was <15 km from its closest anthropogenic roost sites. When landfills are more distant from anthropogenic roost sites, commuting costs to these landfills may outweigh the benefits derived from feeding there. Alternatively, ravens feeding at landfills may roost at closer anthropogenic roost sites to minimize the amount of travel required to reach that landfill the following day.

Landfills with anthropogenic roosting locations nearby (<15 km) were used heavily in the latter part of the day, but few ravens were foraging late in the afternoon. I hypothesize that landfills close to anthropogenic roosts (<15 km away) are used as staging areas for ravens as they congregate before roosting at night. The amount of loafing at the Kemmerer landfill recorded during the afternoon was significantly greater than in the morning; ravens perched within the landfill facing the nearest roost locations. In contrast, landfills >20 km from the nearest anthropogenic roost site did not see increases in ravens at the end of the day.

Environmental patterns affected how often raven used landfills for foraging and anthropogenic structures for roosting; raven use of these sites increased when temperatures decreased and precipitation increased, although precipitation was an imprecise predictor of roost size. Ravens have difficulty locating concealed food items
(Heinrich 1988), and falling snow may obscure other food sources from view. Preston (2005) found an increase in the numbers of ravens visiting a landfill 58 km away from a roost when temperature decreased and snow depth increased. In Jackson Hole, WY, a severe winter buried road-killed carcasses, drastically limited available natural food resources, and promoted an influx of ravens into the local landfills during the winter (Dorn 1972).

Roosting in large numbers (>150 ravens) in protected and/or heated locations may be a way for ravens to conserve heat. Some of my documented roosts had heat sources, and ravens roosted close to the heated elements in roosts during winter. In unheated roost sites, ravens were observed roosting shoulder to shoulder. In Alaska, oil field workers interviewed in Alaska’s North Slope about raven behavior almost always linked heated structures with their raven observations, and 71% of the workers reported heavy use of processing facilities by ravens in the winter (Backensto 2010). One smaller raven roost in an abandoned building ($\bar{x} = 72$ ravens) in eastern Canada was used by more ravens when wind chill increased during the winter (Watts et al. 1991). Therefore, it appears that winter weather increases raven use of anthropogenic structures with shelter or heat for roosts.

After leaving winter locations, raven dispersal distances in this study ($\bar{x} = 38$ km) were significantly less than band recovery distances for wintering ravens in Iceland ($\bar{x} = 151$ km; Skarphédinsson et al. 1990) and Greenland (median distance = 30, 70, and 73 km for 3 study sites; Restani et al. 2001). This average distance suggests that a majority of ravens in southwest Wyoming do not migrate vast distances in the spring, relative to other locations globally. Wyoming has more temperate winters than Iceland and
Greenland, and the agricultural setting provides plentiful food resources (livestock carcasses, insects, etc.) during the spring, rather than frozen tundra. Instead, these ravens are more localized, and they reconvene at landfills and anthropogenic roost sites the following winter, based on the presence of previously radio-marked ravens the following winter.

I found that ravens in winter depended highly on anthropogenic structures for roosting, and although ravens regularly visited landfills, they were not the major site for foraging in the winter. Anthropogenic resources have allowed raven numbers to increase in recent decades (Leu et al. 2008, Saur et al. 2011) by increasing survival and chick production (Kristen et al. 2004, Webb et al. 2004). Winter is a stressful time, and the use of anthropogenic roost sites, landfills, and other human related food sources (road-killed ungulates, gut piles from hunting, etc.) likely improves the chances of survival for ravens. It also may increase the chance of breeding-aged ravens to maintain a stable body condition that will allow more energy resources to go towards reproduction the following spring. Thus, raven populations subsidized in the winter by anthropogenic resources will likely continue to increase if left unchecked. I found that ravens disperse within 40 km, on average, from landfills in the spring and return to these locations in the winter. Although this dispersal radius is relatively small, local populations of sensitive wildlife, livestock operations, and industrial sites are still at risk for raven damage if large numbers of ravens exist.

**MANAGEMENT IMPLICATIONS**

Ravens captured at landfills and next to anthropogenic roost sites stayed within 40 km of where they were captured, and they used these locations on a regular basis during
the winter. Raven management, in order to be effective, must address the winter ecology of ravens. Effectiveness of raven removal may improve during the winter because of the relative ease of selecting certain areas to target, as well as the increased probability of targeting large numbers of ravens. However, raven removal at these sites may not target the raven population as a whole, and ravens foraging at landfills and roosting at anthropogenic sites did not use these locations all of the time. Therefore, winter raven control is a supplement, and not a replacement, to existing raven management practices.

**LITERATURE CITED**


**Table 2-1.** Correlation coefficients ($r$) between the numbers of ravens roosting at anthropogenic structures and the total numbers of raven utilizing landfills for specific roost-landfill pairs in southwest Wyoming, USA, during the winters of 2014 and 2015. The sample sizes of roost counts in the winter of 2013 were small ($n < 10$); therefore, no correlations were conducted that year. I compared 264 concurrent roost and landfill counts.

<table>
<thead>
<tr>
<th>Year</th>
<th>Roost</th>
<th>Kemmerer</th>
<th>Green River</th>
<th>Rock Springs</th>
</tr>
</thead>
<tbody>
<tr>
<td>2014</td>
<td>Port of Entry</td>
<td>0.47</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>2014</td>
<td>Shute Creek</td>
<td>0.06</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>2014</td>
<td>Solvay</td>
<td>0.26</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>2015</td>
<td>Port of Entry/Encana</td>
<td>0.62</td>
<td>0.34</td>
<td>0.09</td>
</tr>
<tr>
<td>2015</td>
<td>Shute Creek</td>
<td>0.31</td>
<td>0.12</td>
<td>0.14</td>
</tr>
<tr>
<td>2015</td>
<td>Solvay</td>
<td>0.20</td>
<td>0.20</td>
<td>0.09</td>
</tr>
</tbody>
</table>

*Landfill not monitored that year*
Table 2-2. Distance (km) between specific pairs of landfills and anthropogenic roosts used by ravens, southwest Wyoming, USA, during the winters of 2014 and 2015.

<table>
<thead>
<tr>
<th>Roost</th>
<th>Kemmerer</th>
<th>Green River</th>
<th>Rock Springs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Port of Entry</td>
<td>7</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Shute Creek</td>
<td>38</td>
<td>67</td>
<td>77</td>
</tr>
<tr>
<td>Solvay</td>
<td>69</td>
<td>23</td>
<td>39</td>
</tr>
<tr>
<td>Port of Entry/Encana</td>
<td>11</td>
<td>95</td>
<td>110</td>
</tr>
</tbody>
</table>

*Landfill not monitored the year the roost was active*
Table 2-3. Proportion of the number of evenings ($N$) that radio-marked ravens ($n = 73$) roosted at particular anthropogenic roost sites the evening after spending that day at certain landfills, southwest Wyoming, USA, 2013-2015.

<table>
<thead>
<tr>
<th>Roost</th>
<th>Landfill</th>
<th>Year</th>
<th>$N$</th>
<th>Viaduct</th>
<th>POE/Encana</th>
<th>Shute Creek</th>
<th>Solvay</th>
<th>Unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Kemmerer</td>
<td>2013</td>
<td>62</td>
<td>84%</td>
<td>*</td>
<td>**</td>
<td>**</td>
<td>16%</td>
</tr>
<tr>
<td></td>
<td>Kemmerer</td>
<td>2014</td>
<td>313</td>
<td>*</td>
<td>84%</td>
<td>8%</td>
<td>0%</td>
<td>9%</td>
</tr>
<tr>
<td></td>
<td>Kemmerer</td>
<td>2015</td>
<td>381</td>
<td>*</td>
<td>80%</td>
<td>3%</td>
<td>0%</td>
<td>17%</td>
</tr>
<tr>
<td></td>
<td>Green River</td>
<td>2015</td>
<td>48</td>
<td>*</td>
<td>2%</td>
<td>0%</td>
<td>71%</td>
<td>27%</td>
</tr>
<tr>
<td></td>
<td>Rock Springs</td>
<td>2015</td>
<td>38</td>
<td>*</td>
<td>0%</td>
<td>0%</td>
<td>66%</td>
<td>34%</td>
</tr>
</tbody>
</table>

*Roost not active that year

**Roost not monitored that year
Table 2-4. Top 15 Poisson generalized linear models assessing the effect of climatic and rhythmic variables on the daily number of ravens utilizing 3 landfills in southwest Wyoming, USA, 2013-2015.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>k</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day length + moonlight + precipitation + Tmax</td>
<td>16921.2</td>
<td>0.0</td>
<td>5</td>
<td>0.98</td>
</tr>
<tr>
<td>Moonlight + precipitation + Tmax</td>
<td>16929.3</td>
<td>8.2</td>
<td>4</td>
<td>0.02</td>
</tr>
<tr>
<td>Day length + precipitation + Tmax</td>
<td>17172.5</td>
<td>251.3</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Precipitation + Tmax</td>
<td>17176.0</td>
<td>254.8</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Moonlight + Tmax</td>
<td>17213.3</td>
<td>292.1</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + moonlight + Tmax</td>
<td>17215.1</td>
<td>293.9</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + Tmax</td>
<td>17713.3</td>
<td>792.1</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Tmax</td>
<td>17233.9</td>
<td>802.7</td>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + moonlight + precipitation</td>
<td>19363.4</td>
<td>2442.2</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + precipitation</td>
<td>19382.9</td>
<td>2461.7</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Moonlight + precipitation</td>
<td>19616.9</td>
<td>2695.7</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Precipitation</td>
<td>19628.8</td>
<td>2707.6</td>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + moonlight</td>
<td>20435.4</td>
<td>3514.2</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Moonlight</td>
<td>20546.7</td>
<td>3635.6</td>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length</td>
<td>20620.3</td>
<td>3699.1</td>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td>Intercept-only</td>
<td>20701.2</td>
<td>3780.0</td>
<td>1</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Table 2-5. Parameter estimates for the top AIC$_c$ selected model explaining environmental variables that influence the daily number of ravens utilizing 3 landfills in southwest WY, USA, 2013-2015.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>95% Lower CI</th>
<th>95% Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>5.500</td>
<td>0.080</td>
<td>4.785</td>
<td>6.204*</td>
</tr>
<tr>
<td>Day length</td>
<td>-0.602</td>
<td>0.188</td>
<td>-2.324</td>
<td>1.064</td>
</tr>
<tr>
<td>Moonlight</td>
<td>0.316</td>
<td>0.020</td>
<td>0.029</td>
<td>0.582*</td>
</tr>
<tr>
<td>Precipitation</td>
<td>0.297</td>
<td>0.017</td>
<td>0.077</td>
<td>0.524*</td>
</tr>
<tr>
<td>Tmax</td>
<td>-0.062</td>
<td>0.001</td>
<td>-0.076</td>
<td>-0.049*</td>
</tr>
</tbody>
</table>

* Denotes parameter estimates where the 95% confidence intervals do not include zero.
Table 2-6. Top 15 binomial generalized linear models assessing the effects of environmental variables on the numbers of ravens roosting at 5 anthropogenic roost sites in southwest Wyoming, USA, 2013-2015.

<table>
<thead>
<tr>
<th>Model</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$k$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moonlight + precipitation + Tmin</td>
<td>28949.0</td>
<td>0.0</td>
<td>4</td>
<td>0.69</td>
</tr>
<tr>
<td>Day length + moonlight + precipitation + Tmin</td>
<td>28950.6</td>
<td>1.6</td>
<td>5</td>
<td>0.31</td>
</tr>
<tr>
<td>Precipitation + Tmin</td>
<td>28962.6</td>
<td>13.6</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + precipitation + Tmin</td>
<td>28964.1</td>
<td>15.1</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Moonlight + Tmin</td>
<td>29082.9</td>
<td>133.8</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + moonlight + Tmin</td>
<td>29083.0</td>
<td>134.0</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Tmin</td>
<td>29100.8</td>
<td>151.8</td>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + Tmin</td>
<td>29100.8</td>
<td>151.8</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + precipitation</td>
<td>30419.8</td>
<td>1470.8</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + moonlight + precipitation</td>
<td>30421.8</td>
<td>1472.8</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Precipitation</td>
<td>30492.6</td>
<td>1543.5</td>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td>Moonlight + precipitation</td>
<td>30494.5</td>
<td>1545.5</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length</td>
<td>30525.6</td>
<td>1576.6</td>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td>Day length + moonlight</td>
<td>30527.6</td>
<td>1578.6</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Intercept-only</td>
<td>30584.6</td>
<td>1635.5</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Moonlight</td>
<td>30586.5</td>
<td>1637.5</td>
<td>2</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Table 2-7. Model-averaged parameter estimates for the top 2 models containing 90% of the AIC<sub>c</sub> weight for environmental variables influencing the numbers of ravens roosting at 5 anthropogenic roost sites in southwest WY, USA, 2013-2015.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>95% Lower CI</th>
<th>95% Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>5.513</td>
<td>0.075</td>
<td>5.376</td>
<td>5.672*</td>
</tr>
<tr>
<td>Day length</td>
<td>0.021</td>
<td>0.820</td>
<td>-1.252</td>
<td>1.314</td>
</tr>
<tr>
<td>Moonlight</td>
<td>0.040</td>
<td>0.089</td>
<td>-0.133</td>
<td>0.222</td>
</tr>
<tr>
<td>Precipitation</td>
<td>0.118</td>
<td>0.079</td>
<td>-0.049</td>
<td>0.265</td>
</tr>
<tr>
<td>Tmin</td>
<td>-0.023</td>
<td>0.004</td>
<td>-0.031</td>
<td>-0.014*</td>
</tr>
</tbody>
</table>

* Denotes parameter estimates where the 95% confidence intervals do not include zero.
Figure 2-1. Map of the study area, showing the locations of 5 anthropogenic roosts and 3 landfills used by ravens in southwest Wyoming during the winter months (November-March) from 2013-2015. Map shows major highways in the region. The Kemmerer area is enlarged to show detail.
Figure 2-2. Numbers of ravens attending the Kemmerer landfill and roosting at anthropogenic roost sites during the winter of 2013-2014 on concurrent days in southwest Wyoming, USA.
Figure 2-3. Numbers of ravens attending the Kemmerer landfill and roosting at anthropogenic roost sites during the winter of 2014-2015 on concurrent days in southwest Wyoming, USA.
Figure 2-4. Numbers of ravens attending the Green River landfill and roosting at anthropogenic roost sites during the winter of 2014-2015 on concurrent days in southwest Wyoming, USA.
Figure 2-5. Numbers of ravens attending the Rock Springs landfill and roosting at anthropogenic roost sites during the winter of 2014-2015 on concurrent days in southwest Wyoming, USA.
Figure 2-6. Hourly mean (SE) of the numbers of ravens utilizing landfills during the winter in southwest Wyoming, USA, 2013-2015. Data were available for the Kemmerer landfill and Green River landfill from November-March; the Rock Springs landfill had data from January-March.
Figure 2-7. Hourly mean (SE) of the hourly percentages of radio-marked ravens out of the daily total number of marked ravens ($n = 73$) that visited landfills during the winter in southwest Wyoming, USA, 2013-2015. Data were available for the Kemmerer and Green River landfills from November-March; the Rock Springs landfill had data from January-March.
Figure 2-8. Hourly percentages of ravens (SE), out of the total number of ravens present at landfill counts, foraging at three landfills during the winter months in southwest Wyoming, USA, 2015.
Figure 2-9. Spring dispersal locations ($n = 51$) for very-high frequency (VHF) radio-marked ravens captured in southwest Wyoming, USA, 2013-2015. The 3 large open circles represent capture locations.
Figure 2-10. Spring dispersal locations ($n = 1,383$) for 5 global positioning system (GPS) radio-marked ravens captured in southwest Wyoming, 2015. Raven 146186 was captured at the Green River landfill (right capture location), whereas the other 4 ravens were captured at the Kemmerer landfill (left capture location).
CHAPTER 3
EFFECTIVENESS OF THE TOXICANT DRC-1339 FOR MANAGING
POPULATIONS OF COMMON RAVENS IN WYOMING

ABSTRACT Common raven (*Corvus corax*) populations have increased several fold in the western United States during the last century; these birds cause problems when they kill new-born livestock and prey on threatened species. The toxicant DRC-1339 is used by USDA/APHIS Wildlife Services (WS) to manage common raven populations. Due to the slow-acting nature of the toxicant, it is difficult to determine the numbers of ravens killed. I examined the effectiveness of DRC-1339 applications for preventative control of ravens at 3 landfills and 5 nearby roosts in southwest Wyoming from 2013 through 2015. WS removed 23%, 34%, and 7% of the radio-marked sample of ravens during the winters of 2013, 2014, and 2015, respectively. Raven population estimates did not significantly decline from the 2013 winter to the 2014 winter and from the 2014 winter to the 2015 winter. Ravens did not avoid landfills after DRC-1339 applications, yet roost switching increased in the week following DRC-1339 applications, compared to the prior week. Estimated mortality rates from DRC-1339 applications based on carcass counts underestimated the actual rates by 79%, and counts of ravens at landfills and other treatment areas underestimated them by 49%. Roost count estimates of mortality were within 15% of the actual mortality rates. Therefore, roost counts are the preferred technique for estimating raven mortality due to DRC-1339 when a population of radio-tagged ravens is unavailable.
INTRODUCTION

Common raven (Corvus corax; hereafter raven) populations have increased several fold in the western U.S. during the last several decades (Boarman 1993, Boarman and Berry 1995, Sauer et al. 2011). These enlarged populations are managed using toxicants for the protection of human health, livestock, and wildlife species, including desert tortoise (Geopherus agassizii) and greater sage-grouse (Centrocercus urophasianus; hereafter sage-grouse). Often the preferred toxicant is 3-chloro-p-toluidine hydrochloride (DRC-1339) because ravens are more susceptible to it than many other avian species or mammals (Decino et al. 1966). DRC-1339 is slow-acting, causing death 3-50 hours after ingestion (Decino et al. 1966). This toxin is often injected into chicken eggs or sprayed on dog food, which is then used as bait. These treated baits are then distributed where they will be consumed by ravens that are causing problems, often after a pre-baiting program so that the local raven are used to consuming the bait.

Removal efforts using DRC-1339 have varied in long-term effectiveness. Larsen and Dietrich (1970) found only 10 ravens (5% of the original population) at the treatment site the year following application. In contrast, raven numbers returned to pre-treatment levels in Nevada 1 year after treatment, indicating that the raven population at large was not affected by the previous year’s raven take (Coates et al. 2007). An intensive removal program in Iceland removed an average of 4,116 common ravens annually from 1981-1985; the number of breeding pairs did not fluctuate significantly during this time period, but a decline in the non-breeding population was observed (Skarphédinsson et al. 1990).

The long delay between ingestion of DRC-1339 and death makes it difficult to determine how many ravens are killed during an application of the toxicant. Techniques
used to monitor raven mortality after an application of DRC-1339 vary considerably, and include estimating mortality from bait consumption, carcasses searches, and raven counts before and after a DRC-1339 application. Coates et al. (2007) assessed raven take by estimating that 1 raven died for every 11 poisoned eggs that disappeared or were eaten. Butchko (1990) conducted extensive searches in the landfill where eggs treated with DRC-1339 were distributed and retrieved 78 raven carcasses; he used this number, combined with the number of shot ravens, to calculate the mortality rate. Larsen and Dietrich (1970) never reported finding any raven carcasses in their study area after using DCR-1339, only that ravens were absent at the lambing grounds. However, the presence of dead or dying ravens after a DRC-1339 application may deter ravens from returning to baited areas so counting ravens at baiting sites may overestimate the number of ravens killed (Merrell 2012, Peterson and Colwell 2014). With a plethora of methods available, it is important to identify which method(s) most accurately describe raven mortality.

In southwest Wyoming, large-scale raven management by USDA/APHIS Wildlife Services (WS) was employed in the winters of 2013-2015 to protect livestock and human health from ravens. In this study, I monitored the DRC-1339 program’s effectiveness in reducing raven numbers. Another goal of this study was to determine if ravens learned to avoid areas where DRC-1339 was applied or local roosts. I also tested 3 methods to determine which one(s) provided the best estimates of raven mortality: carcass counts, counts at treatment areas, and roost counts.

**STUDY AREA**

I monitored raven activity at 3 landfills and 5 large (̅ >150 ravens) roosts in Lincoln and Sweetwater counties, in southwest Wyoming, during the winter months (1
November – 31 March) from 2013-2015 (Fig. 3-1). The Kemmerer landfill was monitored all 3 years, and it was where most ravens were captured for radio-marking. Garbage at this landfill was packaged into large bales, stacked in an open pit, and covered with approximately 15 cm of dirt most days. However, the sides of the newest rows of bales were left exposed and available for raven foraging. I also captured ravens at the Green River and Rock Springs landfills and monitored them for raven activity after the discovery of radio-marked ravens at these locations in November 2014 and January 2015, respectively. Both of these landfills utilized a “loose-fill” approach: garbage was dumped into an open pit, crushed with a compactor, and covered with approximately 15 cm of dirt 2 to 3 times a week.

My study area in rural Wyoming lacked large groves of trees suitable for roosting in the winter months. Instead, ravens roosted at industrial sites or under bridges. From the winters of 2013-2015, I monitored 5 raven roosts, all within 30 km of the nearest landfill. Roost sites were all man-made, including railroad bridges and industrial sites. Roost sites differed from year to year.

The study area encompassed approximately 2,500 km², and the elevation was, on average, 2,100 m. The habitat surrounding the landfills was largely composed of sagebrush (*Artemisia* spp.) plant communities. Agricultural use was limited to mainly cattle and sheep grazing across the study area; most land was managed for multiple-use by the Bureau of Land Management (BLM). Oil and gas sequestration composed the highest land use activity outside of agriculture. During the winter months from 2013-2015, Kemmerer received an average of 6 cm of precipitation, and daily temperatures
averaged -4 °C. Green River and Rock Springs received 7 cm of precipitation from November 2014 to March 2015; daily temperatures averaged -0.1 °C.

METHODS

All applications of DCR-1339 were conducted by WS from January to the end of March (2014 and 2015) or April (2013). I was verbally notified of the removal plan at the beginning of every year from WS; I was updated as to the timing of a DCR-1339 application as the date got closer. WS personnel used dried dog food (Hi-Standard® 26/18 Soy Free Premium Performance Dog Food, Hi-Standard Dog Food, Pinckneyville, IL) as the primary bait for their applications. This dog food was then treated with DRC-1339 by spreading the dog food onto a flat surface and using a spray bottle of diluted DRC-1339 to obtain the desired application rate specified by the U.S. Environmental Protection Agency label. The lethal dose of DRC-1339 that will kill 50% of the ravens (LD₅₀) is 13 mg/kg of body weight (Larsen and Dietrich 1970, Eisemann et al. 2003, Homan et al. 2005). Once bait was treated, it was distributed either alone or mixed with untreated dog food at landfills, next to roosts, on estimated flight paths <2 km from roosts, or in areas experiencing raven problems (e.g. lambing grounds or natural gas sequestration tanks). The amount of bait placed out during a removal event was correlated to the estimated number of ravens visiting the treatment area. Bait was placed mostly on the ground; however, feeding troughs were sometimes attached to perching locations (i.e. snow fences) to distribute bait. Employee effort (i.e., man-hours) fluctuated because of the amount of time spent pre-baiting. Hence, the number of man-hours was monitored as a reflection of how much a site was pre-baited.
I captured ravens using #3 leg-hold traps (Oneida Victor® Soft Catch® Coil, Euclid, OH) placed within landfills and near road-kills or carcasses next to roosts. Raven capture locations were concentrated where WS targeted ravens for removal. Captured ravens were equipped with either 19- or 24-g VHF backpack transmitters (Model A1135/A1140, Advanced Telemetry Systems, Isanti, MN) or 30-g solar-powered GPS PTT transmitters (North Star Science and Technology, King George, VA). All ravens were released at their capture site as soon as the transmitters were attached. These methods were approved by the Institutional Animal Care and Use Committee of Utah State University (Protocol number 2031), the U.S. Fish and Wildlife Service (banding permit #21175), and the Wyoming Game and Fish Department (Chapter 33 Permit #657).

Stationary data loggers (Model 4500S, Advanced Telemetry Systems, Insanti, MN) equipped with 3-element Yagi antennae (Communications Specialists, Orange, CA) recorded telemetry data for radio-marked ravens on a continual basis. Data loggers picked up radio-marked ravens 1 km from where they were positioned based on field testing and cross-testing with hand-held receivers. I programmed the data-loggers to detect transmitter frequencies and to store them for subsequent downloading. I utilized Communications Specialists (Communications Specialists, R-1000, Orange, CA) receivers and 3-element Yagi antennae at landfills (throughout the day) and at roosts (once each night after all roosting ravens were present) where data loggers were not stationed.

Ravens equipped with the GPS transmitters were monitored on a daily basis using data collected from Argos satellites. Six points per raven per day were collected at 0000, 0700, 1000, 1300, 1600, and 1900 MST. Most (98%) of the days contained ≥1 GPS
location fix for each raven equipped with a GPS transmitter. Solar charging issues (e.g. feathers covering the solar cell) contributed to most of the lost fixes (2%).

Radio-marked ravens were monitored at roosts and landfills during the DRC-1339 application period and during the months before and after application at roost and landfill locations. I used these radio-marked ravens as an accurate estimate of survival for the raven population at large. I then compared this estimated mortality rate with rates determined using carcass, landfill, and roost counts to assess which counts more accurately represented the actual mortality rate. Each winter, the survival of radio-marked birds was recorded weekly starting when the first ravens were captured and ending in April or May when I conducted aerial flights to locate all radio-marked ravens. Ravens that survived this period were considered to have survived the winter. I defined a removal period as the period of time from the first DRC-1339 application to a week after the last DRC-1339 application. In 2013, the removal period went from 27 February-11 April. However, data logger data were only available after 7 March. In 2014, the removal period went from 17 January-12 March, and the data loggers were available throughout the entire period. In 2015, the removal period went from 21 January-10 February. Roost attendance and landfill attendance were monitored constantly throughout the removal periods from 2013-2015.

Apparent survival was defined as the proportion of radio-marked birds known to be alive at the start of winter that were also alive at its end. The apparent survival rate does not show variability in mortality rates or explain how raven survival varies throughout the entire removal period. A Kaplan-Meier estimator (Kaplan and Meier 1958) was used to estimate weekly survival from the first raven capture in the winter to
the last telemetry flight in the spring. The Kaplan-Meier estimate is an accepted survival estimator that can be applied to telemetry data obtained from radio-marked animals (Pollock et al. 1989). The Kaplan-Meier estimator is the non-parametric maximum likelihood estimation of survival, \( S(t) \), where the maximum survival is calculated over the set of all piecewise survival curves with breakpoints at the event times \( t_i \) (in this case, weeks). It is expressed as:

\[
S(t) = \prod_{t_i < t} (1 - d_i / r_i)
\]

In this equation, \( r_i \) is the number of ravens at risk just prior to time \( t_i \). The number at risk fluctuates with regard to death; if a raven died one week, it cannot be at risk in subsequent weeks. Right censoring, where ravens were not located weeks before survival monitoring ended, also is accounted for in the Kaplan-Meier estimator; the number at risk drops after an individual raven disappears from the study. Thus, \( r_i \) is the number of survivors minus the number of losses, either due to death or disappearance. The number at risk also fluctuates with staggered entrance; in my study, ravens entered the study area at different time periods. The parameter \( d_i \) represents the number of deaths at time \( t_i \).

From 2013 to 2015, roost counts at all known roosts on similar dates were tallied together to observe changes in the raven population. Telemetry data were used to calculate the number of radio-marked ravens present at each roost night, and these were used in conjunction with the number of ravens counted in roosts on similar nights to calculate the total number of ravens in the population. I divided the sum of the roost counts by the detection probability, or the proportion of radio-marked birds known to be alive that were at the roost(s) at the time of the roost counts.
I monitored if radio-tagged ravens abandoned landfills after DRC-1339 applications. Nearly all raven carcasses (95%) were retrieved within a week of each DRC-1339 application. With these data in mind, the daily percentages of marked ravens at landfills one week after DRC-1339 applications were subtracted from the daily percentages of marked ravens at the onset of DRC-1339 applications to estimate what percentage of ravens abandoned landfills after DRC-1339 applications.

I monitored how often radio-marked ravens switched from one roost to another during the removal period to determine if ravens responded to DRC-1339 applications by switching roosts. American crows (*Corvus brachyrhynchos*), a similar corvid species, relocated to a new roost after DRC-1339 was distributed at the staging area of the former roost (Boyd and Hall 1987). Roost switching occurred when a raven moved from one roost to another on consecutive nights. Roost switching was only observed during the winters of 2014 and 2015. I did not consider ravens moving between the Port of Entry roost and the Encana roost as switching roosts because movement of birds between these 2 roosts occurred frequently. These two roosts were close together (12 km) whereas the rest of the roosts were separated by 40 to 80 km.

I compared the number radio-marked ravens that were known to be alive that switched roosts one week before each DRC-1339 application and one week following that same DRC-1339 application. In this analysis, each individual raven was the sampling unit, and a single raven may have been alive during several applications of DCR-1339. To avoid pseudo-replication, I calculated the proportion of times a raven switched roost during the 1-week pre-application period to the proportion during the 1-week post-application period. Sometimes, dead ravens were found on the ground below a
roost after a DRC-1339 application. To determine the effect of dead ravens on roost switching, I compared the proportion of times a raven switched roosts when there was a dead raven at a roost to when there were no dead ravens. I used the Wilcoxon’s signed rank test to test whether a DRC-1339 application or a raven carcass affected how frequently ravens switch roosts.

The recovery of raven carcasses provides concrete evidence that ravens died. Raven carcasses were regularly collected by plant staff and researchers after DRC-1339 applications to estimate the number of ravens killed. I searched for raven carcasses at landfills, roosts, and treatment sites every 1-2 days following a DRC-1339 application, while carcass searches were performed once a week during weeks absent of DRC-1339 applications. Searches were conducted within the landfill boundaries and on the perimeter fences, at the staging areas of roosts, within the roosts themselves, and at treatment sites outside of landfills and roosts. Raven carcasses were also recovered outside of treatment areas with the aid of reports from the public, carcass checks on highways for road-killed ravens, or radio-telemetry. Intensive carcass retrieval did not occur in the winter of 2013.

Treatment and post-treatment counts of ravens at landfills and other treatment areas can be used to monitor how many ravens are being removed by WS. Treatments refer to particular days when WS applied DRC-1339 at a site (landfill or roost) for the purpose of raven removal. Post-treatment data are based on the 3-day time period that it takes for ravens to succumb to DRC-1339 (Decino et al. 1966). I analyzed landfill counts on the date of application with landfill counts on the third day after DRC-1339 was distributed. I monitored ravens during the winter removal periods at 3 landfills targeted
by WS (Kemmerer, Green River, and Rock Springs) multiple times per week to assess changes in raven numbers within each removal year and among removal years. Landfill counts were conducted every 15 min, and most surveys lasted from dawn until a few hours before dark. Treatment and post-treatment counts were created using daily maximum counts. WS activities outside of landfills were conducted on short notice in response to complaints, and I did not reach locations on time to count ravens before application. Therefore, treatment and post-treatment count data in foraging areas outside of landfills was provided by WS. WS also reported treatment and post-treatment count data for 2013; no intensive landfill counts were conducted that year during the removal period. If landfills showed increases in raven numbers from treatment to post-treatment counts, no mortality estimates were recorded for that particular DRC-1339 application.

I determined the number of different ravens using a landfill during a day by creating an index of raven counts that incorporated the detection rate of radio-tagged ravens, and using this number to adjust the maximum number of ravens counted at any given day. I did so by noting how many of the radio-marked ravens were present at the time of the maximum raven count and how many visited the landfill that day, regardless of when they were there. I then divided the maximum raven count by the detection probability of radio-marked ravens at the time of the count. To determine how many ravens were killed by an application of DRC-1339 based on landfill counts, I subtracted the daily number of ravens using the landfill 3 days after an application from the number of ravens prior to the application. The 3 day time period was used to represent the amount of time it takes for a raven to die from DRC-1339 (Decino et al. 1966).
Evening roost counts were conducted 1-2 times per a week at the 5 roosts within the study area. Surveys consisted of counting individual ravens as they entered the roost or associated staging areas. Counts began 1-2 hours before dusk, before most ravens arrived, and continued until darkness prevented further counting. These roost counts were used to assess how many ravens were killed by an application of DCR-1339 by comparing the number of ravens immediately prior to an application to the number 3 days after an application.

RESULTS

When all roosts were combined, the estimated population size for the study area peaked at 2,363, 2,146, and 1,886 ravens during 2013, 2014, and 2015, respectively (Fig. 3-2). I captured and radio-marked 73 ravens from 2013-2015; sample sizes of radio-marked ravens known to be alive during the winter, and thus used in this study, were 23 (2013), 32 (2014), and 34 (2015). WS personnel applied 34, 43, and 30 g of DRC-1339 in treated dog food at our study sites and spent 14, 68, and 32 hours of labor during the 2013, 2014, and 2015 removal periods, respectively. Fifteen radio-marked ravens died during the DRC-1339 applications; eleven of them were recovered at roosts in the days immediately following applications of DRC-1339. During all 3 years of survival monitoring in the winter, only 1 radio-marked raven was killed by something other than DRC-1339; the exception was killed by a mammalian predator. Apparent survival rates of radio-tagged ravens during this study period were 78%, 70%, and 94% in 2013, 2014, and 2015, respectively.

Estimated raven survival during DRC-1339 applications, based on the Kaplan-Meier estimator, was 77% (95% CI = 63% to 97%) during the winter of 2013. The
Kaplan-Meier curve shows that all of the mortality observed occurred during a 3-week period when WS applied DRC-1339 (Fig. 3-3). The survival rate during the winter of 2014 was 66% (95% CI = 50% to 88%). Mortality occurred during the first week of DRC-1339 application, and the survival curve gradually declined throughout the rest of the study (Fig. 3-4). The third year of study (winter of 2015) had a survival rate of 93% (95% CI = 84% to 100%). Mortalities occurred during and immediately after DRC-1339 applications (Fig. 3-5). Using my model, the estimated number of ravens killed from DRC applications during 2013, 2014, and 2015 were 543, 730, and 132 ravens, respectively.

I collected 240 raven carcasses during our study; only five died from causes other than poisoning (three were electrocuted on power poles and two died from vehicle collisions). Most raven carcasses (91%) were retrieved at roosts, <1% of carcasses were recovered at landfills or other sites where DCR-1339 was distributed. I retrieved 221 and 19 carcasses during the winter of 2014 and 2015, respectively.

On average, 9% (95% CI = -23% to 41%) of the radio-marked ravens present at the onset of DRC-1339 applications abandoned landfills within a week after DRC-1339 was applied. Seven of 51 (14%) radio-marked ravens switched roosts the week before a DRC-1339 application, and 14 of 51 (28%) radio-marked ravens switched roosts in the week immediately following each application. Roost switching of individual ravens was more prevalent a week after a DRC-1339 application than in the week preceding it ($W = 4.0$, $P = 0.02$). The presence or absence of dead ravens on the ground below a roost did not influence the number of ravens that switched roosts ($W = 10.5$, $P = 0.32$).
Based on maximum raven counts at landfills and other treatment areas, an estimated 240, 288, and 93 ravens were killed by DRC-1339 during the winter of 2013, 2014, and 2015, respectively. When these values were adjusted for the proportion of radio-marked ravens present at the time of maximum count at landfills, 338, 559, and 160 ravens were killed by DRC-1339 during the winter of 2013, 2014, and 2015, respectively. Based on roost counts, an estimated 462, 619, and 153 ravens were killed by DRC-1339 during the winter of 2013, 2014, and 2015, respectively.

**DISCUSSION**

WS removed 7-34% of a raven population of approximately 2,000 ravens with DRC-1339 by killing 132-730 ravens each winter in Sweetwater and Lincoln counties of Wyoming. Population size over a wide geographical area is rarely reported in a raven removal study. However, when compared to raven removal elsewhere in the United States, the winter kill by DRC-1339 in our study area ($\bar{x} = 468$ ravens annually in a 2,500 km$^2$ area = 0.18 ravens/km$^2$) was lower than the amount of ravens removed by Larsen and Dietrich (1970) at lambing grounds [190 ravens in a 4 km$^2$ area = 47.5 ravens/km$^2$], the number of ravens removed in Butchko’s (1990) study (115 ravens in a 106 km$^2$ area = 1.08 ravens/km$^2$), and Coates et al. (2007) estimated to have killed at sage-grouse leks ($\bar{x} = 161$ ravens annually in a 100 km$^2$ area = 4.22 ravens/km$^2$). The approach WS took in southwest Wyoming was to kill large numbers of ravens in the winter to prevent problems during the spring; therefore, they concentrated their removal efforts on multiple roosts and landfills when ravens heavily utilized these locations. The previously mentioned studies had all of their control efforts concentrated in the spring at specific sites to kill ravens that were causing damage at the time of application.
Preventative control over a large area, due to the large number of damage complaints in the past, was the goal of WS in southwest Wyoming. However, as WS removed ravens at roosts and landfills, they likely targeted a subset of ravens that utilized roosts and landfills on a regular basis. Ravens did not always use these locations during the winter (see Chapter 2), and certain ravens could be avoiding these areas in favor of different areas (e.g. ungulate wintering grounds, major highways). Therefore, the number of ravens killed per unit area may be less than other studies because of the concentration of removal activity by WS in a small number of locations, in comparison to a large study area.

Raven mortality rose with an increase in man-hours and DRC-1339 applied by WS. Distributing more treated bait likely improved the likelihood of ravens finding it, as well as giving more ravens the chance to eat the treated bait. The increase in man-hours was spent mainly by pre-baiting.

During my study, most mortalities (93%) of our radio-tagged ravens were due to the ingestion of DCR-1339. Likewise almost all (98%) dead ravens that we found died of DCR-1339 poisoning. Raven populations, based on combined roost counts during subsequent winters, did not significantly decline after every poisoning year. The maximum raven population at my roosts and landfills in southwest Wyoming dropped by 9% from the 2013 winter to the 2014 winter, and the raven population dropped 12% from the 2014 winter to the 2015 winter; however, significant variation was seen in the estimated population size (Fig. 3-1). Raven populations can be hard to depress. In Iceland, an annual take exceeding 4,000 ravens did not decrease the raven populations a year later annually (Skarphéadinsson et al. 1990). Over 10,560 chicken eggs (2,640 per
year) treated with DRC-1339 were distributed near sage-grouse leks in Nevada from 2002-2005; even with this massive removal effort, raven indices at these leks rebounded back to the same levels or increased the following year (Coates et al. 2007). In southwest Wyoming, ravens have an unlimited supply of anthropogenic food, which provides plentiful resources for reproductive success. Kristen et al. (2004) showed that ravens in the West Mojave Desert have increased recruitment rates when their diets were enhanced by trash, roadkill, and other anthropogenic food resources. Webb et al. (2004) also documented increased juvenile raven survival in the same study site when nests were closer to anthropogenic resources. With a plethora of resources at hand, high fecundity rates of the surviving ravens and high recruitment rates of juvenile ravens to the breeding population likely offsets the losses observed the previous poisoning year. Immigration of individuals from areas outside of landfills and roosts may have also occurred; raven population increases in the Mojave Desert have been linked with ravens being drawn in from surrounding area (Fleischer et al. 2008). In conclusion, preventative raven control during the winter, if continued in southwest Wyoming, will likely result in short term reductions with minimal multi-year effects.

I hypothesized that ravens would learn to avoid landfills and roosts after an applicant of DRC-1339 because ravens often avoid areas where they observe dead ravens (Merrill 2012, Peterson and Colwell 2014). Instead, I found that radio-marked ravens did not stop foraging at treated landfills following the application of DRC-1339. Apparently the surviving ravens did not associate the increase in mortality rates with foraging at landfills. This may have resulted because a raven can take up to 3 days to succumb to DRC-1339 after ingestion (Decino et al. 1966); therefore, it has ample time to travel
away from where it ingested the bait. In fact, I only found 2 of 238 raven carcasses at landfills. Instead, most carcasses were retrieved from roosts areas and in the sagebrush >2 km away from landfills. Thus, ravens may not perceive danger at landfills, due to the lack of mortality observed at these locations. In support of this hypothesis, Coates et al. (2007) did not find video evidence of avoidance behavior by ravens of eggs treated with DRC-1339. However, ravens switched roosts more often after a DRC-1339 application; I witnessed abnormal behavior (e.g. flying into roost structures, laying down on the ground below the roost) by dying ravens at roosts while collecting raven carcasses. This behavior may startle healthy ravens and encourage the use of another roost.

Estimates of raven mortality, based on carcass counts, were 79% lower, on average, than our mortality estimates calculated from the radio-marked ravens. Most of these ravens died away from roads and in remote terrain. Carcass retrieval outside of treatment areas would be time-consuming and costly, because the search area exponentially increases as the search radius from the treatment areas increases. Outside of radio-telemetry, carcass retrieval in southwest Wyoming is an inefficient method for assessing raven take.

Raven mortality estimates based on raw landfill and treatment area counts were 49% lower than estimates obtained from raven survival data in all 3 years of the study. In my study, radio-marked ravens attended landfills at different times of the day, suggesting that a maximum count of ravens at one point in time does not truly estimate the total numbers of ravens utilizing the landfill on a daily basis. Ravens also are inconsistent in the time of day they forage at lambing grounds, agricultural areas, and other areas where ravens regularly visit (Larsen and Dietrich 1970, Engel and Young 1992). I conclude that
use of raw counts of ravens at landfills and other treatment sites is an inefficient method for assessing raven mortality in southwest Wyoming.

Raven mortality estimates based on counts in local roosts differed by an average of 15% from estimates provided the Kaplan-Meier estimator. Hence, I conclude that raven counts at roosts provided the better estimate of population changes caused by poisoning than landfill/treatment area counts or carcass counts.

MANAGEMENT IMPLICATIONS

Raven management with DRC-1339, when used in a preventative manner before problems arise, can be used to depress raven populations; however, it is a short-term solution that must be conducted annually. Reducing anthropogenic sources of raven food will likely improve removal efforts by increasing raven attendance at treatment sites; regularly picking up road-kill and limiting access to landfills are just a few methods that should be explored. Pre-baiting at sites of raven congregation will increase raven kill; however, with regards to protection of other wildlife species (e.g. sage-grouse), it should be done away from areas where the species of interest are congregated (e.g. sage-grouse leks) or during times when these species are less susceptible to raven depredation (e.g. winter) to avoid drawing in ravens from other locations and increasing depredation risk.

LITERATURE CITED


Figure 3-1. Map of the study area showing the locations of 5 roosts and 3 landfills used by radio-marked ravens, southwest Wyoming, USA, 2012-2015. Map includes major roads. The Kemmerer area is enlarged to show detail.
Figure 3-2. Estimated winter raven population sizes based on combined winter/spring roost count data and telemetry data, southwest Wyoming, USA, 2012-2015.
Figure 3-3. Kaplan-Meier survival curve (black line), with 95% confidence intervals (dashed lines) depicting weekly survival of radio-marked ravens, southwest Wyoming, USA, 2012-2013. The survival time started from the first week of raven capture (3 January-7 January) and ended the last week when spring dispersal telemetry flights were conducted (22 May-28 May). Arrows indicate weeks when WS applied DRC-1339 to control ravens.
Figure 3-4. Kaplan-Meier survival curve (black line), with 95% confidence intervals (dashed lines) depicting weekly survival of radio-marked ravens, southwest Wyoming, USA, 2013-2014. The survival time started from the first week of raven capture (15 November - 22 November) and ended the last week when spring dispersal telemetry flights were conducted (16 May - 22 May). Arrows indicate weeks when WS applied DRC-1339 to control ravens.
Figure 3-5. Kaplan-Meier survival curve (black line), with 95% confidence intervals (dashed lines) depicting weekly survival of radio-marked ravens, southwest Wyoming, USA, 2014-2015. The survival time started from the first week of raven capture (9 November-15 November) and ended the last week when spring dispersal telemetry flights were conducted (24 May-30 May). Arrows indicate weeks when WS applied DRC-1339 to control ravens.
CHAPTER 4
THE EFFECTS OF COMMON RAVEN REMOVAL ON SAGE-GROUSE LEK COUNTS IN WYOMING

ABSTRACT Removal of common ravens (*Corvus corax*; raven hereafter) can reduce nest depredations of Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse hereafter); however, the effects of raven removal on sage-grouse abundance have not been explored. I assessed changes in raven density and sage-grouse densities by counting sage-grouse at leks in Wyoming from 2009-2015. We compared areas where USDA/APHIS Wildlife Services (WS) removed ravens (removal areas) to other areas where they did not (non-removal areas). I hypothesized that lek counts would increase from the year before in areas where WS lowered the abundance of ravens. I conducted 6,255 point counts at 1,154 random locations to assess raven densities. In removal areas, raven densities declined 50% from 2008-2014, while raven densities at non-removal areas increased 41% concomitantly. Both preventative raven control in winter at anthropogenic roost sites and landfills and corrective control near livestock were responsible for reducing raven densities at removal sites. Lek counts at removal areas were equal to or lower than non-removal areas from 2009-2012. But, after 2013, when raven removal efforts intensified, this reversed, and lek counts at removal areas were higher than lek counts at non-removal areas. Sage-grouse lek counts increased 0.2% for every 1% decline in raven density the year prior to the count. However, change in raven density was an imprecise predictor of lek counts, while precipitation during winter and August the year prior to lek counts were more informative predictors. Raven removal tailored for livestock protection and human health alone will not influence sage-grouse
INTRODUCTION

Methods to control predators to benefit Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are controversial and vary with regard to the predator species. In Utah’s Strawberry Valley, survival rates and brood success of sage-grouse increased after USDA/APHIS Wildlife Services (WS) started killing red fox (*Vulpes vulpes*) and common ravens (*Corvus corax*; hereafter raven; Baxter et al. 2007). In contrast, Mezquida et al. (2006) speculated coyote (*Canis latrans*) control would negatively affect sage-grouse populations, due to coyote reduction facilitating increases in red fox abundance.

Ravens are significant predators of sage-grouse nests and chicks (Allred 1942, Batterson and Morse 1948, Coates et al. 2008, Bui et al. 2010, Coates and Delehanty 2010, Dinkins 2013). In response to this raven threat, raven removal has been implemented to aid the recovery of sage-grouse populations. Raven control in areas inhabited by sage-grouse has been conducted in the past primarily to protect livestock, especially neonates (Larsen and Dietrich 1970, Spencer 2002), and to address human health and safety concerns, such as fecal contamination in industrial areas and aggressive behavior towards humans (Engel et al. 1992, Merrell 2012). Raven removal efforts often involve applying DRC-1339 to baits, such as meat cubes, chicken eggs, and dog food, and distributing treated bait at areas where ravens are causing problems. DRC-1339 is an avicide that has been used to control pest bird species, including American crows (*Corvus brachyrhynchos*), European starlings (*Sturnus vulgaris*), and ravens (Eisemann et al. 2007).
After being consumed by a bird, DRC-1339’s toxicant, 3-chloro-p-toluidine hydrochloride, causes kidney failure, resulting in death within 3 to 50 hours (Decino et al. 1966).

Due to its promising effectiveness, DRC-1339 has been used extensively for raven removal. Reductions in raven abundance up to 90% were documented after DRC-1339 applications in a large sheep (*Ovis aries*) ranch in Oregon, and lamb depredations dropped by 82% (Larsen and Dietrich 1970). However, control efforts for ravens and other corvids have had, at best, mixed results when trying to augment bird species. In Norway, corvid removal reduced nest losses for black grouse (*Tetrao tetrix*) and willow ptarmington (*Lagopus lagopus*) at removal sites, when compared to control sites, yet this reduction did not show any result in an increase in either bird population (Parker 1984).

Côté and Sutherland (1997) found through meta-analysis that predator control for generalist predators, including ravens, improved nest success and post-breeding population size of several species of birds. More specifically, corvid removal increased productivity of prey species, such as sandhill cranes (*Grus canadensis*) and Eurasian curlews (*Numenius arquata*), yet had minimal effects on the abundance of prey species (Madden et al. 2015).

Reduced raven numbers, as a result of raven removal, may benefit sage-grouse in the short-term. Batterson and Morse (1948) experimentally removed ravens for the benefit of sage-grouse; they reported a 51% nest success rate in the treatment area, compared to a 6% nest success rate in a non-treated area. Coates (2007) found that the number of ravens counted along transects in Nevada dropped to near zero after DRC-1339 applications. An increase of 1 raven per 10 km of transect increased the odds of
sage-grouse nest failure by 7.4% (Coates and Delehanty 2010). In southwestern Wyoming, raven densities declined in raven removal study sites where WS applied DRC-1339 and increased in non-removal study sites (Dinkins 2013). Sage-grouse nest success was 22% when ravens were spotted ≤550 m of a nest and 41% when ravens were not detected. These studies suggest that nesting success of sage-grouse was negatively associated with raven occupancy and/or abundance. However, none of these studies addressed the effects of raven abundance on sage-grouse population growth or decline; there is a need to determine whether sage-grouse abundance increases as a result of reductions in raven abundance after raven removal efforts.

Every year, male sage-grouse congregate and display at strutting grounds, called ‘leks,’ to breed with females. Long-term sage-grouse lek counts have been ongoing within southwestern Wyoming since the 1950s as a means of assessing sage-grouse population trends. Standard protocols are employed to minimize error and bias of these counts, yet there is criticism of the technique (Walsh et al. 2004). Nevertheless, lek counts are often the only long-term data that are consistently available to wildlife agencies (Connelly et al. 2000).

Lek counts, analyzed in relation to raven density fluctuations and removal efforts conducted by WS, provide a means to assess whether sage-grouse populations benefit from raven control. In southwest Wyoming, USDA/APHIS Wildlife Services (WS) removed ravens for the protection of livestock and health and human safety from 2008–2014. I hypothesized that sage-grouse lek counts in this region would be higher in areas where WS lowered the abundance of ravens. To test this hypothesis, I assessed changes
in raven density with changes in sage-grouse lek counts in areas associated with WS raven removal efforts and areas farther away.

STUDY AREA

My study area was located in southwestern and south-central Wyoming and was composed of 12 study sites encompassing 4 counties – Lincoln, Sweetwater, Unita, and Carbon counties – and nearly 345,000 ha (Fig. 4-1). Eight of the study sites were 16 km in diameter, whereas the remaining 4 were 24 km in diameter. Each study site was centralized around ≥1 sage-grouse lek. Size was based on a radial distance of 8.5 km that was determined by Holloran and Anderson (2005) to contain 93% of known sage hen nests from a lek in Wyoming. Study sites were assigned as either removal or non-removal based on their proximity to WS removal activity. Study sites ≤15 km of WS corrective removal and ≤38 km of preventative removal were considered to be ‘removal study sites.’ Study sites outside of these boundaries were considered ‘non-removal study sites.’ There were 2 more removal study sites than Dinkins (2013) designated for his sage-grouse nest success study; however, raven removal resulted in mortality of radio-marked ravens at these study sites during the latter part of the study. Corrective control by WS involved removing offending ravens after they started causing problems (e.g. ravens removed at lambing grounds where producers experienced losses), whereas preventative control involved removing large numbers of ravens at congregation areas (e.g. landfills and anthropogenic roost sites), usually during the winter, to prevent problems from occurring later.
Descriptions of the topography, weather, and vegetation, are described by Dinkins et al. (2012). Land use by agriculture and industry is also described by Dinkins et al. (2012).

METHODS

Data Acquisition

WS initiated raven control during 2007 in Carbon, Lincoln and Sweetwater counties and during 2008 in Uinta County (Rod Merrell, USDA/APHIS WS District Supervisor, personal communication). Most removal activities from 2007 to 2012 were employed in a corrective manner to protect livestock, although preventative control of ravens also occurred (Table 4-1). During 2013, preventative control of ravens was used to respond to the large number of complaints from agriculture and industry. Concomitantly, efforts to remove ravens intensified. WS raven removal methods varied as personnel saw fit in a removal situation. Some initial removal events involved shooting problem ravens with shotguns; however, due to the wariness of ravens following these events and the relative ineffectiveness of this technique (only 57 ravens were shot during 2008–2011 in Carbon, Lincoln, Sweetwater, and Uinta counties), shooting was abandoned as a means of raven removal. DRC-1339 was the toxicant of choice in all other removal events. DRC-1339 was applied to chicken eggs, meat cubes, and dog food; however, dog food in southwest Wyoming was the bait of choice (Rod Merrell, personal communication). Each spatiotemporal removal activity by Wildlife Services was considered a ‘removal event.’
I conducted avian point counts annually at random locations within each study site within sage-grouse nesting and brood-rearing habitat from 2008–2014 to estimate raven densities at each study site. Point-count methodologies are described in detail by Dinkins et al. (2012). To assess the efficacy of WS raven removal with regard to raven densities, I constructed spatiotemporal variables to describe the number of removal events around random point count locations during 2008–2014. The distance to the nearest removal event within the prior 3 and 6 months was calculated for each point count location with ArcMap 10.3. The total number of corrective and preventative removal events within the prior 3 and 6 months were calculated for each point count location with ArcMap 10.3. Corrective removal events were calculated at 7 km, 15 km, and 25 km from a point count location (Dinkins 2013). I adapted the 7-km (154 km²), 15-km (706 km²), and 25-km (1962 km²) search radii around point-count locations to correspond with documented raven home-range size (California 0.3–46 km² [Linz et al. 1992], Minnesota 27–195 km² [Bruggers 1988]), average daily movements (Mojave Desert 4.5 km [Boarman et al. 1995], Idaho 7 km [>95% of movements within 12.5 km; Engel and Young 1992]), and roaming distances (Minnesota average 1,252 km² [Bruggers 1988], Maine >1,800 km² [Heinrich 1988], and Michigan average radius 27 km [range 3–147 km; Boarman and Heinrich 1999]). Small distances reflect movements of breeding pairs, whereas larger distances are reflective of the movements of non-breeding individuals.

To determine how far ravens move from preventative control events, I captured ravens at landfills and roosts targeted for raven removal and equipped them with 19-g or 20-g VHF transmitters (Model A1135/A1140, Advanced Telemetry Systems, Insanti,
MN). I obtained 51 spring locations of ravens from 2013-2015 using aerial telemetry. Most ravens were located from 15 May to 31 May, with one flight conducted in the last week in April. These data were augmented with daily GPS data collected from April to May 2015 from 5 ravens fitted with 30-g solar-powered GPS transmitters (North Star Science and Technology, LLC, King George, VA) in 2015. All ravens were released at their capture site as soon as the transmitters were attached. These methods were approved by the Institutional Animal Care and Use Committee of Utah State University (Protocol number 2031), the U.S Fish and Wildlife Service (banding permit #21175) and the Wyoming Game and Fish Department (WGFD hereafter; Chapter 33 Permit #657).

During the spring, ravens moved, on average, 38 km away from the landfill where they were captured (Chapter 2). Hence, the number of preventative removal events for each point count location was calculated by summing all of the preventative removal events that occurred within 38 km of that location.

WGFD, BLM, and volunteer personnel counted male sage-grouse at leks in years concurrent with this project. Lek count surveys were conducted based on protocols developed by the WGFD. These protocols standardize Wyoming lek counts to minimize bias associated with timing, weather conditions, proximity to other known leks, and other factors that could affect the validity of these counts. I designated lek complexes as a series of leks within 2.5 km of the largest, most regularly attended lek to account for sage-grouse male interchange between leks (Connelly et al. 2004). Lek complexes, under my definition, refer to a single lek or multiple leks; hereafter, we refer both simply as leks. I also determined the proportion of counts at a lek that were ‘trend counts’ or
‘survey counts.’ ‘Trend counts’ were conducted under rigorous protocols to standardize count procedures, whereas ‘survey counts’ were conducted with less effort.

Leks within my study sites or bordering (≤300 m away) study sites were used to compare with my raven densities quantified in removal and non-removal study sites. Comparisons were possible because sage-grouse hens nest within the vicinity of the leks where they are bred (Holloran and Anderson 2005), and raven depredations of sage-grouse nests likely occurred within our study sites. Female sage-grouse chicks often nest near their natal nest when they mature (Thompson 2012), and female sage-grouse tend have high nest-site fidelity (Berry and Eng 1985, Fischer et al. 1993). Additionally, male sage-grouse juveniles often display at their natal-area lek, and once sage-grouse males reach maturity, they often revisit the same lek every year (Dunn and Braun 1985, Schroeder and Robb 2003). Therefore, eggs and chicks depredated by ravens in these study sites likely contribute to recruitment of sage-grouse within these study sites.

Recruitment in sage-grouse populations was highly influenced by annual climatic variation in Idaho, Nevada, and Utah (Blomberg et al. 2012, Guttery et al. 2013). Therefore, I incorporated weather into my models to account for variation other than raven removal. I obtained monthly maximum temperature, minimum temperature, and precipitation variables from Parameter-elevation Regressions on Independent Slopes Model (PRISM) data (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 1 March 2015); weather stations were not distributed evenly across all study sites. Weather variables were constructed on a seasonal (winter and summer) basis; winter was defined as running from 1 November to 31 March, based on the time when most precipitation fell as snow in our study sites.
Summer was defined as running from 1 May to 31 August to correspond with the timing of sage-grouse nesting and brood rearing seasons. Summer climatic variation was analyzed monthly; Guttery et al. (2013) found summer monthly precipitation and temperature data fit models better than summer seasonal data.

**Statistical Analyses**

I implemented a spatiotemporal modeling strategy to evaluate trends in 1) the effect of WS removal activities on raven abundance and 2) the effect of study site level raven abundance and climatic variation on sage-grouse lek counts. A spatiotemporal strategy was implemented because many variables describing raven abundance and sage-grouse lek counts pertain to a given year or study site. Modeling of raven abundance and sage-grouse lek counts were conducted with an information theoretic approach (Anderson 2008); I compared models with Akaike’s information criterion adjusted for sample size ($\text{AIC}_c$) and Akaike weights ($w_i$; Burnham and Anderson 2002). For simplicity, I discussed the top $\text{AIC}_c$ selected models unless model averaging was useful for models that contained comparable variables and whose weights were distributed widely across several models (Burnham and Anderson 2002, Arnold 2010). I detected multicollinearity for all pairs of variables by using a Pearson’s correlation matrix; I did not include variables in the same model if $r \geq 0.50$.

I used function ‘gdistsamp’ in package UNMARKED version 0.10-6 (Fiske and Chandler 2011) in R (R 3.2.2, www.r-project.org, accessed 1 September 2015) to model the effects of year, year trend, and removal-event variables on the density of ravens in removal and non-removal study sites. The ‘gdistsamp’ function fits a multinomial-Poisson mixture model (Royle et al. 2004) that allows for analysis of standard distance
sampling data (Ralph et al. 1995, Thomas et al. 2010) at discrete distance intervals, while simultaneously modeling detection and abundance. In my models, I created 250-m distance intervals and right truncated data at 1950 m to best fit the data. Several key functions described by Dinkins (2013) were fit to my models; ‘gdistsamp’ models with hazard-rate key detection functions fit the data best. I accounted for survey effort by incorporating the number of visits per point count location as an offset. I assessed annual raven abundance within removal and non-removal study sites by modeling year and year trend; these 2 variables were not compared in the same model. In WS-removal models, I included distance to the nearest removal event, number of corrective removal events, and number of preventative removal events. I used 95% confidence intervals (CI) generated from ‘distsmap’ to compare parameter estimates from top AICc selected models.

Sage-grouse lek counts were analyzed using generalized linear models (GLMs) in Program R. A Poisson distribution was used because it best describes count data that does not contain excessive zero counts or negative values. Study-site level raven densities from the top AICc models in the previous analyses were incorporated into the modelling process. Raven densities were analyzed with a year time-lag because juvenile males entering leks would have been targeted as eggs and chicks by ravens the previous nesting season. I looked at the percent change in study-site level raven density with respect to the raven density at each study site in the beginning of the study. For example, the percent change in raven density at all study sites was 0 in 2008. I also looked at the effect of study-site type (removal versus non-removal) on sage-grouse lek counts; however, I did not include this variable in models with percent change in raven density because of autocorrelation. Weather variables were incorporated in the models with a
year time lag, similar to the raven density variable construction, and they were Z-standardized, similar to how Guttery et al. (2013) transformed climate variables. I adjusted the lek count data by incorporating, as an offset, the proportion of counts in a single lek year that were ‘trend counts’. I constructed 95% confidence intervals by bootstrapping over 5,000 replicates.

RESULTS

WS raven removal efforts, from 2007 to 2009, were mostly directed toward corrective control for livestock protection, and preventative control was minimal (Table 4-1). After 2010, preventative raven control increased substantially, declined in 2011 and 2012, and increased again the last two years of the study. Corrective raven control fluctuated similarly, yet it contributed to a lower percentage of removal events in 2014, due to the lack of complaints from livestock producers in the spring (Rod Merrell personal communication).

I conducted 6,255 raven point-count surveys (3,618 removal site surveys, 2,637 non-removal site surveys) from 2008-2014 at 1,154 random locations (636 removal site locations and 518 non-removal site locations). I counted 1,675 ravens during point-count surveys (1,106 in removal sites and 569 in non-removal sites). The nearest distance from a point count to a WS removal event was, on average, 17.7 km and 45.2 km at removal and non-removal study sites, respectively.

In my models describing raven abundance, I found that the year trend models out-competed both the year models in removal and non-removal study sites. In non-removal study sites, the year trend model was an imprecise predictor of raven density, but year trend did contribute to describing the data (Tables 4-2 and 4-3). Raven densities
decreased 50% from 2008-2014 in removal study sites, whereas raven densities increased in non-removal study sites by 41% (Table 4-3, Fig. 4-2). In my models describing WS removal events at removal study sites, the top models that held most of the model weight and were within 2 AICc of each other included number of corrective removal events within 15 km, number of preventative removal events, and distance to the nearest removal event; removal variables calculated at 6 months fit better than removal variables at 3 months. Removal study sites were best described by the number of preventative removal events (Tables 4-4 and 4-5, Fig. 4-3). The number of corrective control events within 15 km was an imprecise predictor of raven densities; however, it contributed to describing the data (Tables 4-4 and 4-5, Fig. 4-3). Distance to the nearest removal event was not an informative predictor of raven densities at removal study sites (Tables 4-4 and 4-5). None of the removal event variables adequately described raven densities at non-removal study sites; the null model was highly competitive with the top WS removal models (Table 4-4).

I analyzed count data at 58 sage-grouse leks in southwest Wyoming (30 in removal study sites and 28 in non-removal study sites). Sage-grouse lek counts at removal and non-removal study sites were similar in 2009 (Fig. 4-4). From 2010-2012, lek counts, on average, were lower at removal study sites than counts at non-removal study sites (Fig. 4-4). From 2013-2015, lek counts at removal study sites were higher, on average, than counts at non-removal study sites (Fig. 4-4). The top-selected AICc model describing lek counts included site-specific percent change in raven density, winter precipitation, and August precipitation; no models were competitive with it (Table 4-6). I found that increases in raven density had negative effects on lek counts; a 1% increase in
site-specific raven density resulted in a 0.2% decline in lek counts within that study site. Site-specific change in raven density was an imprecise predictor of change in sage-grouse lek counts (95% CI = -0.5 to 0.2%); however, it contributed to describing the data (Table 4-7, Fig. 4-5).

Winter precipitation had positive effects on sage-grouse lek counts; an increase in 1 unit in the Z-score from the mean total winter precipitation at a particular study site was associated with a 17% increase (95% CI = 6-29%) in sage-grouse lek counts (Table 4-7, Fig. 4-5). August precipitation was positively correlated with sage-grouse lek counts; an increase in 1 unit in the Z-score from the mean total precipitation in August was associated with a 13% (95% CI = 3-25%) increase in sage-grouse lek counts (Table 4-7, Fig. 4-5).

DISCUSSION

This study was one of the few that examined the effect of raven removal on sage-grouse lek counts. It also was unique in using multiple removal and non-removal sites. Raven densities dropped 50% in removal study sites from 2008-2014, whereas raven densities at non-removal study sites increased 41% over the same time period. WS removal models demonstrated that increases in the number of preventative and corrective removal events over a 6-month period best described the observed drops in raven densities at removal study sites. These results demonstrate that raven removal can drop raven densities within sage-grouse nesting habitat for an extended period of time, provided that raven removal is conducted every year.

The drop in raven densities at removal sites was associated with increases in sage-grouse lek counts. Lek counts were positively associated with study site-level declines in
raven densities the year prior to the count. It is probable that suppressed raven densities reduced the proportion of sage-grouse nests depredated by ravens; Dinkins (2013) found decreased nest success with an increase in raven occupancy near sage-grouse nest sites in this project’s area from 2008-2011. This increased productivity of sage-grouse could have resulted in increasing the number of surviving male chicks that were seen the following spring at sage-grouse leks. Sage-grouse hens avoid visual predators, including ravens, and prefer to nest in areas with lower densities of ravens (Dinkins et al. 2012, Dinkins et al. 2014). Thus, a decline in landscape-level raven densities may have opened up more suitable nesting habitat for sage-grouse hens and contributed to successful brood-rearing.

However, the effect that changes in raven densities had on sage-grouse lek counts were not seen until 2013-2015, when raven densities the year prior were >35% less than raven densities at the start of the study. I hypothesize that this was due to increased intensity of preventative raven control in the latter years of the study. In 2013 and 2014, preventative raven control was higher than most years except 2010 (Table 4-1), and preventative control was the strongest predictor of declines in raven density (Table 4-5). Large drops in raven density are likely needed to decrease sage-grouse nest depredation by ravens because ravens are generalist predators that do not rely on sage-grouse for prey (Schroader and Baydack 2001, Coates 2007).

In contrast, the effects of weather on sage-grouse lek counts were at least a degree of magnitude larger, compared to the effects of changing raven densities. Increased winter precipitation and August precipitation was correlated with increases in sage-grouse lek counts the following year. Increased snowpack can increase sage-grouse
recruitment by increasing the available soil moisture (Blomberg et al. 2012), which increases the abundance of insects and forbs in the spring (Wenninger and Inouye 2008); these are important food sources for juvenile and adult sage-grouse (Klebenow and Gray 1968, Barnett and Crawford 1994, Gregg et al. 2006, Gregg and Crawford 2009, Connelly et al. 2011).

In the western US, especially in Wyoming, summers are hot and dry, and soil moisture likely is depleted after July. Increased August precipitation may be important in maintaining soil moisture levels for forb production; juvenile sage-grouse are more apt to forage on forbs in the fall (Klebenow and Gray 1968, Huwer 2004), and these forbs are also substantial components in the diets of hens in the fall (Wallestad and Eng 1975). It may also be beneficial for late-starting broods that rely heavily on insects for their first few weeks of life; insect abundances are higher in the fall when there is an abundance of moisture (Wenninger and Inouye 2008). Of course, wildlife biologists can reduce raven numbers but cannot do anything to change the weather.

In general, raven removal is believed to be a short-term solution to aid sage-grouse populations in peril (Coates 2007, Bui et al. 2010, Hagen 2011, Dinkins 2013). I agree that raven removal would be most beneficial for sage-grouse populations that are low in numbers and in areas where subsidized raven densities are high. Other options would be to harass ravens at landfills and anthropogenic roost sites in the winter. These methods would make it harder for ravens to find food and encourage ravens to roost in less desirable locations, which could also decrease raven abundance. Different methods, such as effigies, non-lethal shooting, lethal shooting, and pyrotechnics, are promising solutions for deterring ravens from landfills and roosting locations, provided they are
implemented correctly and in conjunction with each other (DeFusco 2007. Merrell 2012, Peterson and Colwell 2014).

**MANAGEMENT IMPLICATIONS**

In this study, both preventative removal and corrective removal explain declines in raven densities where sage-grouse were nesting, yet corrective control was an imprecise predictor. In this study, raven removal was used to protect livestock and human health. Raven management will likely be more effective if corrective control is tailored to benefit sage-grouse. One example is to distribute DRC-1339 treated eggs within proximity of sage-grouse nesting habitat (Coates 2007). However, corrective control is more costly than preventative control because ravens are dispersed and harder to target in large numbers. I found that ravens in Wyoming travel an average of 38 km from landfills they attended during the winter to their spring nesting and foraging locations. This indicates that preventative removal during the winter is effective in reducing raven abundance in areas <38 km from landfills.

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Table 4-1. Raven removal events conducted by USDA/APHIS Wildlife Services in southwest and south-central Wyoming, USA, 2007–2014. The total number of removal events is reported around removal study sites; this number includes corrective and preventative events. Removal at roosts and landfills were considered to be preventative control events in this study.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total number removal events</th>
<th>DRC-1339 used at livestock calving/lambing grounds</th>
<th>DRC-1339 used at roosts</th>
<th>DRC-1339 used at landfills</th>
<th>Firearms</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>16</td>
<td>12</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2008</td>
<td>9</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>2009</td>
<td>44</td>
<td>38</td>
<td>0</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>2010</td>
<td>40</td>
<td>24</td>
<td>1</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td>2011</td>
<td>27</td>
<td>19</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>2012</td>
<td>29</td>
<td>22</td>
<td>1</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>2013</td>
<td>45</td>
<td>37</td>
<td>1</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>2014</td>
<td>25</td>
<td>12</td>
<td>4</td>
<td>9</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 4-2. Multinomial-Poisson mixture models assessing the effect of year and year trend on raven densities using ‘gdistsamp’ in R. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA, 2008–2014.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$k$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Removal study sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year trend</td>
<td>3882.49</td>
<td>0.00</td>
<td>6</td>
<td>0.63</td>
</tr>
<tr>
<td>Year</td>
<td>3883.56</td>
<td>1.07</td>
<td>11</td>
<td>0.37</td>
</tr>
<tr>
<td>Intercept-only</td>
<td>3896.27</td>
<td>13.78</td>
<td>5</td>
<td>0.00</td>
</tr>
<tr>
<td><strong>Non-removal study sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year trend</td>
<td>2859.82</td>
<td>0.00</td>
<td>6</td>
<td>0.59</td>
</tr>
<tr>
<td>Intercept-only</td>
<td>2860.60</td>
<td>0.79</td>
<td>5</td>
<td>0.40</td>
</tr>
<tr>
<td>Year</td>
<td>2869.33</td>
<td>7.87</td>
<td>11</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Table 4-3. Model-averaged parameter estimates for the top Multinomial-Poisson mixture models within assessing the effect of year trend on raven densities at removal and non-removal study sites using ‘gdistsamp’ in R. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA, 2008–2014.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>95% Lower CI</th>
<th>95% Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Removal study sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.962</td>
<td>0.136</td>
<td>-1.419</td>
<td>-0.958*</td>
</tr>
<tr>
<td>Year trend</td>
<td>-0.116</td>
<td>0.029</td>
<td>-0.119</td>
<td>0.007*</td>
</tr>
<tr>
<td><strong>Non-removal study sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-1.826</td>
<td>0.191</td>
<td>-2.201</td>
<td>-1.451*</td>
</tr>
<tr>
<td>Year trend</td>
<td>0.059</td>
<td>0.034</td>
<td>-0.008</td>
<td>0.126</td>
</tr>
</tbody>
</table>

* Denotes parameter estimates where the 95% confidence intervals do not include zero.
Table 4-4. Multinomial-Poisson mixture models assessing the effect of removal event variables on raven densities using ‘gdistsamp’ in R. Only the top 10 models for removal and non-removal study sites were reported. The temporal scale (3 or 6 months prior to last point count at a random location) of each model is denoted in parenthesis. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA, 2008–2014.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>k</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Removal study sites</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corrective removal 15k + preventative removal (6 months)</td>
<td>3917.16</td>
<td>0.0</td>
<td>6</td>
<td>0.35</td>
</tr>
<tr>
<td>Preventative removal (6 months)</td>
<td>3918.35</td>
<td>1.20</td>
<td>5</td>
<td>0.19</td>
</tr>
<tr>
<td>Corrective removal 15k + preventative removal + removal dist (6 months)</td>
<td>3919.10</td>
<td>1.94</td>
<td>7</td>
<td>0.13</td>
</tr>
<tr>
<td>Corrective removal 7k + preventative removal (6 months)</td>
<td>3919.93</td>
<td>2.77</td>
<td>6</td>
<td>0.09</td>
</tr>
<tr>
<td>Corrective removal 25k + preventative removal + removal dist (6 months)</td>
<td>3919.99</td>
<td>2.83</td>
<td>6</td>
<td>0.09</td>
</tr>
<tr>
<td>Corrective removal 7k + preventative removal + removal dist (6 months)</td>
<td>3920.11</td>
<td>2.95</td>
<td>7</td>
<td>0.08</td>
</tr>
<tr>
<td>Preventative removal (3 months)</td>
<td>3921.21</td>
<td>4.05</td>
<td>7</td>
<td>0.05</td>
</tr>
<tr>
<td>Corrective removal 15k + preventative removal (3 months)</td>
<td>3925.55</td>
<td>8.40</td>
<td>5</td>
<td>0.01</td>
</tr>
<tr>
<td>Corrective removal 25k + preventative removal (3 months)</td>
<td>3926.20</td>
<td>9.04</td>
<td>6</td>
<td>0.00</td>
</tr>
<tr>
<td>Corrective removal 7k + preventative removal (3 months)</td>
<td>3927.57</td>
<td>10.42</td>
<td>6</td>
<td>0.00</td>
</tr>
<tr>
<td>Non-removal study sites</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Removal dist (3 months)</td>
<td>2860.46</td>
<td>0.00</td>
<td>5</td>
<td>0.13</td>
</tr>
<tr>
<td>Removal dist (6 months)</td>
<td>2860.59</td>
<td>0.14</td>
<td>5</td>
<td>0.12</td>
</tr>
<tr>
<td>Intercept-only</td>
<td>2860.60</td>
<td>0.15</td>
<td>4</td>
<td>0.12</td>
</tr>
<tr>
<td>Service</td>
<td>Price</td>
<td>Cost</td>
<td>Hours</td>
<td>Margin</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>--------</td>
<td>-------</td>
<td>-------</td>
<td>---------</td>
</tr>
<tr>
<td>Preventative removal (3 months)</td>
<td>2861.19</td>
<td>0.73</td>
<td>5</td>
<td>0.09</td>
</tr>
<tr>
<td>Corrective removal 25k (6 months)</td>
<td>2861.40</td>
<td>0.94</td>
<td>5</td>
<td>0.08</td>
</tr>
<tr>
<td>Corrective removal 25k (3 months)</td>
<td>2861.81</td>
<td>1.36</td>
<td>5</td>
<td>0.07</td>
</tr>
<tr>
<td>Corrective removal 15k + preventative removal (3 months)</td>
<td>2862.32</td>
<td>1.86</td>
<td>6</td>
<td>0.05</td>
</tr>
<tr>
<td>Corrective removal 15k (6 months)</td>
<td>2862.46</td>
<td>2.00</td>
<td>5</td>
<td>0.05</td>
</tr>
<tr>
<td>Corrective removal 15k (3 months)</td>
<td>2862.46</td>
<td>2.00</td>
<td>5</td>
<td>0.05</td>
</tr>
<tr>
<td>Preventative removal (6 months)</td>
<td>2862.54</td>
<td>2.08</td>
<td>5</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Table 4-5. Model-averaged parameter estimates for the top 3 Multinomial-Poisson mixture models within 2 $\Delta$AIC$_c$ of each other assessing the effect of removal event variables on raven densities at removal study sites using ‘gdistsamp’ in R. The temporal scale of each variable is denoted in parenthesis. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA, 2008–2014.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>95% Lower CI</th>
<th>95% Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.188</td>
<td>0.118</td>
<td>-1.419</td>
<td>-0.958*</td>
</tr>
<tr>
<td>Corrective removal 15k (6 months)</td>
<td>-0.056</td>
<td>0.032</td>
<td>-0.119</td>
<td>0.007</td>
</tr>
<tr>
<td>Preventative removal (6 months)</td>
<td>-0.067</td>
<td>0.014</td>
<td>-0.095</td>
<td>-0.038*</td>
</tr>
<tr>
<td>Distance to removal (6 months)</td>
<td>0.002</td>
<td>0.006</td>
<td>-0.010</td>
<td>0.014</td>
</tr>
</tbody>
</table>

* Denotes parameter estimates where the 95% confidence intervals do not include zero.
Table 4-6. Generalized linear models assessing the effect of study-site level changes in raven density, study site type, and climatic variables, including precipitation (prcp) and temperature (temp), on sage-grouse lek counts using R. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA, during 2008–2014.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>k</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Change in raven density + winter prcp + Aug prcp</td>
<td>10692.8</td>
<td>0.0</td>
<td>4</td>
<td>1.00</td>
</tr>
<tr>
<td>Winter prcp + Aug prcp</td>
<td>10779.3</td>
<td>86.5</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + winter prcp + June min temp</td>
<td>10833.7</td>
<td>140.8</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Study site type + winter prcp</td>
<td>10842.1</td>
<td>149.3</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + May prcp + Aug min temp</td>
<td>10850.8</td>
<td>158.0</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + Jul min temp + Aug min temp</td>
<td>10864.8</td>
<td>172.0</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + May max temp + Aug min temp</td>
<td>10866.5</td>
<td>173.7</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + Jun min temp + Aug min temp</td>
<td>10866.5</td>
<td>173.7</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + winter prcp + Jun max temp</td>
<td>10873.1</td>
<td>180.3</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + Jul prcp + Aug min temp</td>
<td>10875.2</td>
<td>182.4</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + Aug min temp</td>
<td>10877.7</td>
<td>184.9</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + May min temp + Aug min temp</td>
<td>10879.7</td>
<td>186.9</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + Aug prcp + Jun max temp</td>
<td>10885.1</td>
<td>192.3</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Winter prcp + Jun min temp</td>
<td>10891.9</td>
<td>199.0</td>
<td>3</td>
<td>0.00</td>
</tr>
<tr>
<td>Change in raven density + winter prcp + Jul max temp</td>
<td>10901.2</td>
<td>207.3</td>
<td>4</td>
<td>0.00</td>
</tr>
<tr>
<td>Intercept-only</td>
<td>11436.9</td>
<td>744.1</td>
<td>2</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Table 4-7. Parameter estimates for the top generalized linear models assessing the effect of change of raven densities and climatic variables on sage-grouse lek counts. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA, during 2009–2015.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>95% Lower CI</th>
<th>95% Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>2.893</td>
<td>0.050</td>
<td>2.792</td>
<td>2.981*</td>
</tr>
<tr>
<td>Change in raven density</td>
<td>-0.002</td>
<td>0.001</td>
<td>-0.005</td>
<td>0.002</td>
</tr>
<tr>
<td>Winter precipitation</td>
<td>0.162</td>
<td>0.049</td>
<td>0.057</td>
<td>0.253*</td>
</tr>
<tr>
<td>Aug precipitation</td>
<td>0.131</td>
<td>0.047</td>
<td>0.032</td>
<td>0.220*</td>
</tr>
</tbody>
</table>

* Denotes parameter estimates where the 95% confidence intervals do not include zero.
Figure 4-1. Map depicting 8 16-km diameter and 4 24-km diameter study sites, southwestern and south-central, Wyoming, USA, 2008–2014. Map includes study site locations and major roads. Removal study sites are shaded, whereas non-removal study sites are hollow.
**Figure 4-2.** Raven density (#/km$^2$) estimates by year, 2008–2014, from the top AIC$_c$ selected multinomial-Poisson mixture models for removal and non-removal study sites. Error bars indicate 95% confidence intervals. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA.
Figure 4-3. Predictions of raven density (#/km$^2$) from the top AIC$_c$ selected multinomial-Poisson mixture model of USDA/APHIS/Wildlife Services (WS) removal events at removal study sites with 95% confidence intervals. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA, 2008–2014.
Figure 4-4. Average number of males per sage-grouse lek at removal and non-removal study sites with 95% confidence intervals. Data were collected from 12 study sites in southwestern and south-central Wyoming, USA, 2009–2015.
Figure 4-5. Predictions of sage grouse lek counts (number of males per lek) from the top AICc selected Poisson generalized linear model. Predicted effects were made for: A) Site-specific percent change in raven density (#/km²), B) Total amount of winter precipitation, and C) Total amount of August precipitation. Data were collected from 12 study sites in southwestern and south-central, Wyoming, USA, 2009–2015.
The increase in populations of common ravens (*Corvus corax*; raven hereafter) across the western US sparked interest in raven management in areas where ravens threaten young livestock (Larson and Dietrich 1970, Spencer 2002), pose threats to health and human safety (Merrell 2012), and prey upon threatened and endangered species, such as the desert tortoise (*Gopherus agassizii*), California least tern (*Sterna antillarum browni*), and greater sage-grouse (*Centrocercus urophasianus*; sage-grouse hereafter; Linz et al. 1990, Boarman 2003, Coates et al. 2008). A plethora of research has been dedicated to the ecology of ravens and the effectiveness of raven removal in the spring and summer months, when most problems occur. However, little emphasis has been placed on the ecology and control of raven populations during winter in the western US. With regard to sage-grouse, most studies have concentrated on removing ravens near nesting sage-grouse to determine if nest success improves as a result of these removal programs. However, little attention has been given to analyzing the effects of raven removal on sage-grouse abundance.

Raven ecology in winter has not been described in detail in the western US. In Chapter 2, I found that only 22% of ravens within proximity of landfills actually visit these locations on a given day. Ample foraging opportunities on road killed wildlife and dead livestock likely deterred ravens from using landfills more often. Ravens depend on anthropogenic structures for roosting; 68% of the ravens, on average, roost at these locations in the evening. The lack of natural roost substrate in sagebrush (*Artemisia* spp.) dominated habitat left industrial plants and bridges as the only structures available to
accommodate large numbers of ravens. Ravens roosting at anthropogenic structures used landfills at varying degrees. If landfills were <15 km from anthropogenic roosts, ravens foraged at these locations 10-25% more often than at landfills >20 km from the nearest anthropogenic roost site. Increased precipitation and decreased temperatures increased raven attendance at landfills and anthropogenic roost sites. In the spring, ravens dispersed, on average, 38 km from landfills where they were captured.

Due to raven dependency on anthropogenic roost sites, and to some degree landfills, in winter, raven management during winter is potentially a viable option to reduce raven numbers and prevent problems from occurring later, and ravens could be targeted by baiting landfills and anthropogenic roost sites that are <40 km from the area needing protection (see Chapter 2). The toxicant of choice for raven removal is DRC-1339. This toxicant is effective in reducing raven populations in the short-term at locations where ravens cause problems, yet the carryover effects of removal vary immensely (Larson and Dietrich 1970, Coates et al. 2007, Dinkins 2013). Also, the amount of mortality caused by the use of DRC-1339 is questionable. Because ravens learn to avoid dead individuals (Merrell 2012, Peterson and Colwell 2014) and DRC-1339 kills ravens slowly (Decino et al. 1966), raven carcass counts and live counts of surviving ravens could under estimate mortality. In Chapter 3, I monitored raven removal by USDA/APHIS Wildlife Services (WS) at landfills and anthropogenic roost sites during winter. Winter survival of ravens was 23%, 34%, and 7% in 3 years of study, with most death attributed to DRC-1339 applications. Raven population estimates were 9-12% lower the year following winter raven removal. Raven populations can easily rebound from intensive raven removal in human-augmented environments. Raven
reproductive output and survival increases in areas close to landfills, power lines, and paved roads that provide ideal foraging conditions (Kristen et al. 2004, Webb et al. 2004, Steenhof et al. 1993). I found that ravens did not avoid a landfill where DRC-1339 was applied. Only 2 ravens died at a landfill over 3 years, and this low number was insufficient for ravens to learn that landfills were dangerous locations. However, ravens often switched anthropogenic roost sites when DRC-1339 was applied at the roost they were attending. Behavior of ravens dying at the roost likely alarmed non-poisoned ravens and encouraged them to roost elsewhere. Mortality estimates using roost counts were closest (within 15%) to the estimates provided by radio-marked sample. In contrast, carcass counts were 79% lower than telemetry estimates of mortality. The slow acting nature of DRC-1339 and the potential for ravens to die in rough terrain devoid of road access deems carcass counts insufficient to estimate mortality. Landfill counts were 49% lower than telemetry estimates. We found that ravens do not forage or attend landfills simultaneously throughout the day (see Chapter 2). Consequently, using maximum counts at a single point in time does not account for all ravens that use the landfill on a daily basis.

Raven removal has been proposed to help sage-grouse where raven abundance is high. Coates (2007) measured the effects of changing raven densities on sage-grouse nest success in Nevada where raven removal was employed near nesting sage-grouse. His study area included 3 non-removal sites and 1 removal site. He found that raven densities declined to nearly zero at the removal study site. He also found that an increase in 1 raven per 10 km along a transect decreased the odds of nest success by 7.4% (Coates and Delehanty 2010). Dinkins (2013) analyzed raven removal and sage-grouse nest success
in areas where WS conducted removal primarily for the protection of livestock and found that declines in nest-level and landscape-level raven densities improved the daily survival rate of sage-grouse nests. The results presented by Coates (2007) and Dinkins (2013) suggest that sage-grouse reproduction benefits from declines in raven abundance, which is associated with raven removal. Yet, clarification is needed as to whether increased nest success due to raven removal results in changes in population abundance of sage-grouse.

In Chapter 4, I examined how raven removal by WS reduced raven densities and how changes in raven abundance were associated with sage-grouse lek counts. I found that raven densities declined 50% at removal study sites, and this was associated with a combination of preventative control efforts at landfills and anthropogenic roost sites in winter and corrective control efforts at lambing and calving grounds. In contrast, raven densities at non-removal study sites farther away from WS removal increased 41%. Declines in raven densities were correlated with an increase in sage-grouse lek counts, suggesting that sage-grouse populations may have increased by the reduction of raven abundance (see Chapter 4).

Initially, sage-grouse lek counts at removal study sites were lower than lek counts at non-removal study sites, but this changed when raven densities had declined >35% at removal study sites than densities at the start of the study. A 10% decrease in the study-site raven density resulted in a 2% increase in sage-grouse lek counts. These results suggest that raven removal alone will not save sage-grouse populations. Coates (2007), Bui et al. (2010) and Hagen (2011) suggested that raven removal is an interim solution for aiding sage-grouse populations. I agree that the gains in sage-grouse recruitment are short-lived, and other solutions, such as reducing raven access to garbage at landfills,
should be explored further because lethal control has mostly short-term effects on raven populations (see Chapter 3). However, raven removal may play a role in certain scenarios. Sage-grouse populations low in number in fragmented habitat may be pressured by ravens (Braun 1998, Boarman 1993). Reduction of raven abundance in these situations may boost recruitment and result in population increases, in conjunction with other conservation efforts such as habitat maintenance and improvement.

LITERATURE CITED


