NESTING AND POST-FLEDGING ECOLOGY OF THE COMMON RAVEN IN GRAND TETON NATIONAL PARK, WYOMING

An investigation of historical nest density and productivity trends with the study of post-fledging survivorship and departure patterns

A Thesis Presented

By

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to

the Faculty of the Graduate School

of

Arkansas State University

In Partial Fulfillment of the Requirements
for the Degree of Master of Science

August, 2005

General Abstract

The Common Raven (*Corvus corax*) is both geographically and ecologically diverse. However, few studies have investigated demographic trends of this species, and fewer have investigated the causes of mortality and fledgling dispersal movements. From 2002-2004, I monitored a population of ravens in Grand Teton National Park, Wyoming, for population density, productivity, post-fledging survivorship, initial dispersal movements, and fledgling roosting ecology. I also examined historical trends in density and productivity within the study area, and compared these estimates to others for this species, worldwide. I found that the nesting density of Common Ravens in Grand Teton National Park was among the highest densities ever recorded (1 pair/5.3 km^2), while productivity was among the lowest estimates for this species (1.14 fledglings/nest). I found that the nesting density appeared to be related positively to both food augmentation during the fall and early winter months, and an index of human use within the park. I was unable to relate any factors examined to productivity estimates for this population (i.e., nearest-neighbor, distance to nearest human settlement, nest density, elk (*Cervus canadensis*) harvest, and bison (*Bison bison*) herd estimates). Based on radio-telemetry, I found post-fledging survivorship of this population of ravens was relatively high (83%, $n = 62$ fledglings). I found that juvenile survivorship during the post-fledging period was slightly related to nest proximity to the nearest human settlement, but there was no significant relationship to any other potentially influential factor examined. Also, I found that juvenile departures from their natal territories were likely related to food resources both in and outside the territory, with young departing earlier when food was abundant outside of their natal territories. I identified a slight trend that suggested gender biased departure, with females (mean departure = 31.2 days) leaving before their male (mean departure = 37.6 days) counterparts. I also documented that most of the juveniles (67% of family groups, *n* = 19) that departed their territories returned to roost with their parents on their natal territories for a mean of 9.2 nights after their first dispersal movement. My results suggested that this population of Common Ravens was at or near carrying capacity and was partly regulated by density-dependant selection. Further, I suggest that the reproductive strategy evolved in this population can be explained by one of two hypotheses. First, this population may exhibit a relatively K-selection strategy, compared to relatively r-selection utilized by some other raven populations. Alternatively, this population could be “bet hedging,” in that it is better to produce few young that survive in all situations, rather than wasting resources producing many young that will likely not survive in bad years. I suggest this is possible because of few instances of human-related nest failures or mortalities in this population residing in a national park, and because of food subsidies obtained from hunters in the fall and winter (in the form of entrails).

My findings indicated that post-fledging survival can also vary among different populations of this species. I suggest that conservation relying on post-fledging survivorship data must be based on regionally pertinent results that support appropriate local management decisions and strategies. Because of the limited impact of humans in the Grand Teton area, I suggest that my data are useful for comparisons to Common Raven populations that may be strongly influenced by expanding human populations.

Acknowledgments

The culmination of this thesis would not have been possible without the support, encouragement, and efforts of many people. First and foremost, I would like to extend my deepest gratitude to a man that has not only been my mentor, but a close friend since the beginning of this work, Derek Craighead. Without Derek, this project would never have been accomplished, let alone conceived. Derek has taught me about non-assuming respect for others and wildlife, and has provided an exemplary example of a wonderful professional leader. Derek has a deep heart for wildlife and has been one of the most influential people in my life to date.

I would like to thank my graduate committee for their involvement in my academic career. Jeannette Loutsch has shown me the light concerning the methods of cellular and molecular ecology, and patiently held my hand while I learned the hardships and rewards of genetics. My thanks to Tom Risch, who has provoked many interesting ecological ideas and questions throughout my tenure at Arkansas State University (ASU). I am especially grateful to my advisor, Jim Bednarz. Jim has aided me in many aspects of my professional career, as well as sticking through the project, with no selfish interests. Jim has long surpassed my expectations, both as an advisor and as an excellent research ecologist.

This project would not have been completed without the invaluable help from many people out in the field. I wish to extend my gratitude to Nic Osterberg, both a wonderful friend and great colleague. Nic always enthusiastically gathered data, even when it involved being awake at all hours of the night and morning or climbing trees

when he was afraid of heights. I would like to thank Emil McCain for his help and thought provoking questions in the early stages of this project. I would also like to thank Jill Learned, Drea Craighead, Karen Haynam, and Rose Jaffe for their help in the field.

I would like to extend my gratitude to many people in Grand Teton National Park for their help. First, biologist Steve Cain has always provided support for the raven work in the valley, by collecting data that were needed for the historical analysis of this thesis, by lending logistical support, and offering a helping hand. The dispatchers and rangers at the park always aided in finding carcasses for trapping and helped with logistics. I would like to thank Roger Smith for his help in conceiving this project as a thesis and helping me early on. Shirley Craighead provided me not only with nest locations and access to her trees, but also wonderful friendship.

This project would not have been possible without the financial support of the Charles Engelhard Foundation, Community Foundation of Jackson Hole, and the Arkansas Audubon Society. I sincerely thank Sophie Craighead for her support of not only this project, but of my life as a whole. Sophie has been inspiration who always sees the bright side of life and greets me with a warm smile.

My sanity would have been challenged at various times throughout this work, had it not been for the support I received from my many friends and colleagues at ASU. I would like to especially thank Bobby Fokidis, Jill Learned, Ken Levenstein, Drew and Amy Reed, Dean and Kat Townsend, and Hillary Worley. We all spent many hours together in Arkansas keeping each other sane and happy. I am sure each will make a great contribution to the world we live in.

While many of this influential family have already been acknowledged previously, I wish to thank the Craighead Family as a whole. This family has been providing invaluable contributions to ecology and wildlife conservation for generations. I have had help on this project from three generations of Craigheads. Without the early raptor surveys in the park by Frank and John and the follow-up surveys, this thesis would be far less complete. I would like to thank all members of this extended family for their support and respect of wildlife and the systems in which they reside.

To my family, you have always supported my life choices and helped keep me out of trouble. I especially thank my father, without whom, I would be a mechanic at this very moment. I also wish to extend gratitude to my brother James. He has kept my love for this field ever burning, always keeps my mind sharp, and never lets me rest for too long.

And last, but not least, I would like to thank the ravens of Jackson Hole. The cleverness and keenness of these birds never ceases to amaze me. I am forever at their debt for dealing with my presence in their private lives though the past few years and hold them in the highest regard. These birds will always have the upper hand.

Dedication

One of the influential people to my success at this project and to my life has been my wife, Emily. This wonderful woman has stood by my side from the beginning of my budding ecological career and endured many experiences most wives would not. She has never complained about the odd hours I needed to keep for whatever scheme I was working on at the time. She has always put up with dead animals in our freezer, me keeping large dead animals in the back of our truck, and the variety of live animals that seem to end up in our house as well. Emily has shown me understanding and compassion through example and has filled my life with happiness since the day I met her. For all of these reasons, and countless others, I will forever love her.

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Chapter 1

General Introduction

The Common Raven (*Corvus corax*) is geographically and ecologically one of the most diverse bird species in the world, yet little is understood concerning the factors influencing the dynamics of its populations (Dunk et al. 1994; Boarman and Heinrich 1999). Worldwide, there are ten recognized subspecies of Common Ravens, four of which occur in North America. Grand Teton National Park, Wyoming, falls within the range of the subspecies *Corvus corax sinuatus* (Rea 1986*). The range of *C. c. sinuatus* extends from its northmost occupation of southeast British Colombia south to Mexico and Nicaragua. The western portion of the range excludes the states that boarder the Pacific Ocean, and the eastern border occurs in the Great Plains (Boarman and Heinrich 1999).

Ravens experienced population declines in the early twentieth century across much of its range, presumably from poisoning, shooting, and the loss of bison (*Bison bison*; Houston 1977). Range recolonization has been occurring since the mid-twentieth century, and ravens are even considered a pest species in some areas due to their predation on threatened or endangered species (Boarman 1993). In some areas, such as in Virginia, measures have been proposed to protect ravens (Hooper 1977), while areas such as California and Oregon have control programs in place to reduce numbers (Boarman and Heinrich 1999). In areas where ravens are considered pests, the birds are mostly within the range of the *principalis* and *clarionensis* subspecies and are closely associated with anthropogenic resources. In these areas, ravens are not symbols of wilderness and have little fear of humans.

Historically, Common Ravens probably did not occur in the valley of Jackson Hole, Wyoming, which encompasses Grand Teton National Park (GTNP). Ravens were not documented in the valley until 1938 and even then they were only noted in the northern half of Jackson Hole (Stegner 1963*). Ravens were observed as early as 1873 in Teton County, Idaho, which is approximately 600 m lower in elevation than Jackson Hole and occurs adjacent to Teton County, Wyoming, on the west side of the Teton Range (Merriam 1873*). Although Grave and Walker (1916*) considered ravens fairly common throughout northern Wyoming, however, it was not until 1930 that these birds were documented in the Gros Ventre Mountains, which mark the eastern boarder of Jackson Hole (Fuller and Bole 1930*). Raven numbers appeared to have increased dramatically since the first scientific documentation of their nesting densities in the 1940s until the 1970s (Craighead and Mindell 1981).

Raven and raptor populations in the southern portion of GTNP have been scientifically documented within a 31 km^2 area over the past 55 yr (Craighead and Craighead 1956; Craighead and Mindell 1981; Craighead et al. 1987*). The Craigheads (1956) proposed the term “ecological raptor” for ravens because of their observed direct competition with species of *Falconiformes* and *Strigiformes* for nest sites and food. Since the first ecological study (Craighead and Craighead 1956), the density of the Jackson Hole raven population has been periodically monitored (Craighead and Mindell 1981; Craighead et al. 1987*). From the first survey in 1947, when raven nesting density was 0.10 $nests/km^2$ (Craighead and Craighead 1956), there has been a mean increase of

0.0056 nests/year (r^2 = 0.878, P = 0.001). Concurrently, the Red-tailed Hawk (*Buteo jamacensis*) population of GTNP has declined from 0.39 nests/ km^2 in 1947 (Craighead and Craighead 1956) to 0.13 nests/ km^2 (D. Craighead and B. Bedrosian, unpubl. data). This marked decline of hawks was significantly related to the increase of ravens (r^2 = 0.706, P = 0.009), and has raised concerns about the viability of the Red-tailed Hawk population and the interaction of the two species in the protected landscape of GTNP (S. Cain, GTNP Resource Mangmt., pers. comm.).

In order to assess population dynamics of these changing populations, the breeding ecology of the involved species must be understood. While basic productivity studies are useful in comparing populations over time, the data are of limited use in understanding the underlying causes of population dynamics. For example, little is known about the post-fledging ecology of juvenile ravens and factors that influence their success and failure during this period. Furthermore, insight on how many new individuals are recruited into the population as breeders and the number of emigrations and deaths in the population is crucial to understand the dynamics of population change. Also, the influence of food availability on both nest density and the overall success for breeding pairs of ravens may be substantial, but this cause-and-effect relationship has not been evaluated adequately (Dunk et. al 1994).

Clutton-Brock (1988) suggested that in passerines, differential survival of the young during the post-fledging period accounts for much of the variance in parental lifetime reproductive success. Therefore, to understand population changes of long-lived passerines, post-fledging survival needs to be examined. This will not only provide for more accurate productivity estimates, but such data in combination with measures of reproductive success of the population and density can be used to model population growth accurately.

Many factors can influence post-fledging survival. Mortality may be positively related to brood size, due to increased competition with siblings for resources and preferential allocation of food resources by parents (Slagsvold 1984; Husby 1986). Also, smaller broods may be better fed, and therefore beg less, which in turn may attract fewer predators (Ewald and Rohwer 1982; Slagsvold 1982). Conversely, fledgling survival may be correlated with parents' ability to provide adequate care for offspring (Lack 1947; Verhulst and Tinbergen 1991; Brinkohf 1993; Spear and Nur 1994). Often, more experienced breeders nest earlier, have larger clutch sizes, and experience higher reproductive success (Finney and Cooke 1978; Perrins and McClery 1985; Nol and Smith 1987). Post-fledging mortality could also be directly related to hatch order within a brood, because mass at fledging is correlated with hatch order (see Haydock and Ligon 1986; McGrath 1991; Van der Jeugd and Larsson 1998), and therefore, the older nestlings are in better condition than their younger siblings (Krementz et al. 1989). Nests with a later average fledge date may experience a higher mortality due to less time available for maturity before the onset of natal dispersal (Kenward et al. 1993). Finally, Hunt and Hunt (1976) found that birds with a shortened nesting period due to rapid growth, survive better. This may relate to males experiencing better survival than females because of differential growth rates (Krebs 1999).

Following the increase in *C. corax* nests over the past 55 yr, I undertook a 3-yr study of *C. corax* nesting ecology in southern portion of GTNP in 2002. I documented trends in densities and productivity of nesting adults. Also, I collected data that will aid in determining factors that influence nestling and post-fledging survival and dispersal during the breeding season. More specifically, I documented brood sizes, fledging dates, gender, and age within a brood and related these variables to reproductive and fledgling success. This research is notable in that the system being studied has little influence from anthropogenic sources during the breeding season. Because the population resides within a national park, there are no constant human-related food supplies (e.g., landfills, dumpsters), and right-of-ways are extremely limited. Also, I suubmit that this is one of the best examples of an intact ecosystem that is still protected, with species such as elk (*Cervus canadensis*), bison (*Bison bison*), mountain lions (*Felis concolor*), bears (*Ursis americanus* and *U. horribilis*), and wolves (*Canis lupis*) present.

Specifically, this research was designed to address the following questions:

Question 1: What factors are influencing the density of nesting ravens?

Question 2: What factors are influencing the productivity of nesting attempts?

Question 3: What factors affect the longevity of the fledging-dependence period?

Question 4: What is the post-fledging mortality rate and what life history traits influence it?

Question 5: What cause-specific mortality factors affect fledglings?

Question 6: Do the fledglings of Jackson Hole disperse from the valley, suggesting that this population as a source?

To address these questions, I have developed this thesis in manuscript format, in which each manuscript chapter is written to facilitate submission to a scientific journal.

Each chapter will follow the Canadian Field-Naturalist manuscript format, including separate abstract, introduction, methods, results, discussion sections, and be independent of each other.

The first chapter provides a general introduction to this thesis. In the second chapter, I have summarized data on raven nesting density and productivity within the study area, and factors that potentially influence them. I have complied and analyzed over 55 years of nesting and productivity data on ravens in Jackson Hole and compared these estimates to other studies worldwide. I have investigated the potential effects carrion availability in the winter and human use of the area may have on nest timing and productivity. Also, I have explored the potential influence of a non-anthropogenic ecosystem on ravens in comparison with other studies in which ravens are influenced by humans.

In the third chapter, I discuss post-fledging mortality and initial dispersal movements of juvenile ravens. I have investigated the causes of mortality and the timing of these events. I have tested the correlations of brood size, gender, fledging dates, and nest location on mortality. By collecting location data via radio-telemetry of fledglings, I have been able to document dispersal movements and roosting behaviors of the family groups and associations of siblings during the post-fledging dependence period.

Chapter four will cover behavioral observations of the fledglings during the dependence period. I documented roosting behavior of family groups and if food resources affected first dispersal movements. I have also reported a few cases of non-related associations of juveniles after they have dispersed from their natal territories.

I have synthesized all of this research in chapter five, and provided general conclusions concerning this population of ravens. I have also suggested a few management practices for ravens in Jackson Hole, as well as speculating about the health of the population.

Documents Cited (Marked * in text)

Craighead, F. L., F. C. Craighead, Jr., and **J. W. Tischendorf.** 1987. Stability of raptor communities over time. Report. Craighead Environmental Research Institute, Moose, WY.

Fuller, A. B. and **B. P. Bole, Jr.** 1930. Observations on some Wyoming birds. Scientific Publication. Cleveland Museum of Natural History 1: 37-80.

Grave, B. H. and **E. P. Walker.** 1916. Wyoming Birds. University of Wyoming Bulletin 12, No. 16. 137 pp.

Merriam, C.H. 1873. Report on the mammals and birds of the expedition, Pp 661-715. *in* F.V. Hayden, 6th Ann. Rep. U.S. Geological Survey Of Territories. Government Printing Office, Washington, D.C.

Rea. A. M. 1986. *Corvus corax*, geographic variation. Pp. 65-66 *in* The known birds of North and Middle America. Part I. A.R. Phillips, Denver, CO.

Stegner, H. 1963. Grand Teton Nature Notes, 4:8.

Literature Cited

Boarman, W. I. 1993. When a native predator becomes a pest: a case study. Pp. 191-206 *in* S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt and R.

F. Schmalz (eds.). Conservation and resource management. Pennsylvania Academy of Sciences, Easton, Pennsylvania.

Boarman, W. I. and **B. Heinrich.** 1999. Common Raven (*Corvus corax*) *in* The Birds of North America, No 476 (A. Poole and F. Gill, eds.) The Academy of Natural Sciences, Philedelphia, and The American Ornithologists' Union, Washington, D.C.

Brinkhof, M. W. G., A. J. Cave, F. J. Hage, and **S. Verhulst.** 1993. Timing of reproduction and fledging success in the coot *Fulica atra*: evidence for a causal relationship. Jour

Clutton-Brock, T. H. 1988. Reproductive success: Studies of individual variation in contrasting breeding seasons. University of Chicago Press. Chicago.

Craighead, F. C. Jr., and **D. Mindell.** 1981. Nesting raptors in western Wyoming, 1947 and 1975. Journal of Wildlife Management 45: 865-872.

Craighead, J. J., and **F. C. Craighead, Jr.** 1956. Hawks, owls and wildlife. Stackpole, Harrisburg, Pennsylvania.

Dunk, J. R., S. L. Cain, M. E. Reid, and **R. N. Smith.** 1994. A high breeding density of Common Ravens in northwestern Wyoming. Northwestern Naturalist 75: 70-73.

Ewald, P. W. and **S. Rohwer.** 1982. Effects of supplementary feeding on timing of breeding, clutch size and polygny in Red-winged Blackbirds *Agelaius phoeniceus*. Journal of Animal Ecology 51: 429-450.

Finney, G. and **F. Cooke.** 1978. Reproductive habits in the snow goose: the influence of female age. Condor 80: 147-158.

Haydock, J. and **J. D. Ligon.** 1986. Brood reduction in the Chihuahuan Raven: an experimental study. Ecology 67: 1194-1205.

Hooper, R. G. 1977. Nesting habitat of Common Ravens in Virgina. Wilson Bulletin 89: 233-242.

Houston, C. S. 1977. Changing patterns of Corvidae on the prairies. Blue Jay 35: 149-156.

Hunt, G. L. Jr., and **M. W. Hunt.** 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57: 62-75.

Husby, M. 1986. On the adaptive value of brood reduction in birds: experiments with the magpie *Pica pica*. Journal of Animal Ecology 55: 75-83.

Kenward, R. E., V. Marcstrom, and **M. Karlbom.** 1993. Post-nesting behavior in goshawks, *Accipiter gentilis*: I. The causes of dispersal. Animal Behaviour 46: 365-370.

Krebbs, E. A. 1999. Last but not least: nestling growth and survival in asynchronously hatching crimson rosellas. Journal of Animal Ecology 68: 266-281.

Krementz, D. G., J. D. Nichols, and **J. E. Hines.** 1989. Postfledging survival of European Starlings. Ecology 70: 646-655.

Lack, D. 1947. The significance of clutch size. Ibis 89: 302-352.

-------- 1954. The natural regulation of animal numbers. Clarenden Press. Oxford.

Magrath, R. D. 1991. Nestling weiht and juvenile survival in the blackbird, *Turdus merula*. Journal of Animal Ecology 60: 335-351.

Nol, E. and **J. N. M. Smith.** 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. Journal of Animal Ecology 56: 301-313.

Perrins, C. M. and **R. H. McCleery.** 1985. The influence of age and pair bond on the breeding success of great tit *Parus major*. Ibis 127: 306-315.

Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia 54: 159-169.

--------- 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. Journal of Animal Ecology 53: 945-953.

Spear, L. and **N. Nur.** 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. Journal of Animal Ecology 63: 283-298.

Van der Jeugd, H. P. and **K. Larsson.** 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledging characteristics. Journal of Animal Ecology 67: 953-966.

Verhulst, S. and **J. M. Tinbergen.** 1991. Experimental evidence for a causal relationship between timing and reproductive success of the great tit *Parvus m. major*. Journal of Animal Ecology 60: 269-282.

Chapter 2

Examination of Potential Factors Influencing 57-year Nesting Density and Productivity Trends of Common Ravens (*Corvus corax*) in Jackson Hole, Wyoming

Abstract

Common Ravens (*Corvus corax*) have increased in nesting density in a variety of places across North America, but few data exist on factors influencing these population changes. From 2002-2004, I documented nesting density and productivity of ravens in Jackson Hole, Wyoming, and compared these estimates to historical data. I found that the nesting density of ravens in Jackson Hole was among the highest estimates reported for this species, with one of the lowest productivity estimates recorded. These data indicated that this population has been fluctuating around carrying capacity for at least 29 years, and was likely a source population for neighboring populations. I found that the increase of raven nesting density was related to both human visitation to the area and a regional yearly elk (*Cervus candensis*) harvest that provided supplemental food to ravens wintering in the area. I found no relationships between any explanatory variables that I examined and productivity (i.e., nearest neighbor distance, raven nesting density, distance to the nearest human settlement, bison [*Bison bison*] herd estimates).

Introduction

While many researchers have quantified the breeding densities and productivity of Common Ravens (*Corvus corax*) both North America and Europe, none have assessed which factors affect these demographic parameters. Several researchers speculated that raven densities were positively correlated with human settlements (e.g., Dorn 1972*; Hooper 1975; Knight and Kawashima 1993; Restani et al. 2001; Webb et al. 2004), but limited quantitative data were provided to support this notion. Trends of increasing densities are often speculative (e.g., Webb et al. 2004) or rely on indicies that may not reflect actual breeding densities because of ravens' tendencies to be irregularly dispersed, to occur both in large groups and individually, and to wander over large areas (Boarman and Heinrich 1999). Therefore, long-term nesting surveys may be most indicative of population changes, but no such data exist in North America.

Grand Teton National Park (GTNP) resides in Jackson Hole, Wyoming and has limited impact from humans. One of the major human influences on the ecosystem occurs in the form of an annual elk (*Cervus canadensis*) harvest. As would be expected from any large game harvest program, many *grallochs* (discarded entrails) are available for the ravens to feed upon during and after the hunting season. Ratcliffe (1997) and White (2002*) hypothesized that ravens can become conditioned to cue in on gunshots and obtain food rewards from these *grallochs.* Therefore, this learning ability may increase their fitness, especially during the winter, when food is limited in the Jackson Hole area (Dorn 1972*). Likewise, some hunted elk may become crippled and are not recovered by hunters, and these animals later become food bonanzas for ravens.

The raptor community in the mountain valley of Jackson Hole has been censused periodically since 1947 (Craighead and Craighead 1956; Craighead and Mindell 1981; Craighead et al. 1987*; D. Craighead and B. Bedrosian unpubl. data). During these early studies, ravens were considered to be ecological raptors (Craighead and Craighead 1956;

Bednarz et al. 1990) and were included in the surveys. The original 31.1 km^2 survey area examined by Craighead and Craighead (1956) was used in all of these studies have been protected by the Jackson Hole National Monument since 1943, and has had limited modification from human activities during this period. The largest change has been a slow phase out of ranching and agriculture in the area. Given the protection afforded by the National Monument and Grand Teton National Park (which now encompasses this area); I suggest that the raptor community should have been relatively stable across decades. However, the raptor guild has experienced remarkable shifts in population dynamics. Red-tailed Hawks (*Buteo jamecensis*) occurred in very high densities during the 1940s (1 pair/2.6 km^2; Craighead and Craighead 1956), but have subsequently declined (1 pair/7.8 km^2; D. Craighead and B. Bedrosian, unpubl. data). Concurrently, the Common Raven population has experienced the opposite trend, increasing from 1 pair/10.4 km^2 to 1 pair/2.6 km^2 (Craighead and Craighead 1956; D. Craighead and B. Bedrosian, unpubl. data).

The changing population densities of Red-tailed Hawks and ravens may have been facilitated by a number of factors. Given that these two species often live sympatrically and compete for food and nest sites (Craighead and Craighead 1956), a decline in red-tails could have resulted in an increase of resources available to ravens. Because Red-tailed Hawks may favor agriculture and grazed lands for increase visibility of prey (Craighead and Craighead 1956), the slow conversion of the study area to sage/shrub habitat may have hindered the nesting density of red-tails which, in turn opened breeding spaces for ravens. Alternatively, factors fostering an increase in forage for ravens may have caused an increase in their breeding density, which in turn, excluded red-tails from nesting habitat. Little data exist to elucidate the potential effects of interspecific competition between ravens and red-tails.

To better understand these population dynamics, I initiated a detailed study of the nesting population of Common Ravens in Jackson Hole. Using historical data, I was able to examine a 57-year trend in raven nesting density. Also, to avoid biases in estimating nesting densities of ravens from a small study area (Bednarz et al. 1990), I enlarged my survey area beyond the original study area. Common Ravens often rely heavily on anthropogenic resources when available (Knight and Kawashima 1993). Jackson Hole offers a "natural control," in that the ecosystem lacks a point source of anthropogenic subsidy, such as a landfill. Also, this system is complete with the historical predator (*Canis lupis, Urus* spp., and *Felix concolor*) and ungulate communities (*Bison bison, Cervus canadensis, Alces alces, Antilocarpa americana,* and *Odocoileus* spp.) historically associated with ravens (Boarman and Heinrich 1999).

For this study, I assessed the population dynamics resulting from an increasing population of ravens in the Jackson Hole valley. For example, as the nesting density increases, the productivity may decrease due to density dependant factors such as greater competition for resources and greater intraspecific nest predation (Dorn 1972*; Andren 1992; Fernandez et al. 1998). Conversely, the productivity may be correlated with increased density because both may likely be responding to resource availability. Abundant food resources have been shown to support a large number of nests, as well as larger clutch and brood sizes in raptors (Newton 1998). If resources appear limited and productivity is low, this would suggest that this area may be a sink population. If productivity increases with density, then this may indicate that the system has abundant food resources and a key limiting factor would be breeding spaces (Newton 1979). If breeding spaces are limited, ravens may be aggressively competing for Red-tailed Hawk territories.

In long-lived species, McClaren et al. (2002) suggest that reproductive output varies among nest areas, where particular territories consistently produce many or few young based on habitat quality among years. This pattern has been observed for Tengmalm's Owls (*Aegolius funereus*; Korpimaki 1988) and Eurasian Sparrowhawks (*Acippiter nisus*; Newton 1991). To determine if raven territories or nesting pairs produced a consistent number of nestlings, I tested the variation in brood sizes from territories where I had data from multiple years. Further, I tested the prediction that the density of nests would be significantly greater following years with high hunter success due to greater food availability. Also, as an indicator of human presence and potential influence on the nesting density of ravens, I tested the association of density with GTNP human visitation records. In addition, I tested the prediction that ravens have a positive association with bison by relating nesting density with estimates of a bison population that resides within the study area. I also tested the prediction that productivity would be positively related to these variables as well.

Methods

Study Area

The study area encompasses approximately 181 km^2 in the southwest corner of GTNP, which is situated in northwestern Wyoming (43º91'N, 110º40' W; Figure 2.1). Within this study area was the 31 km^2 survey area that was defined by Craighead and

Craighead (1956; hereafter Craighead study area) and the expanded study area used in subsequent raptor surveys of GTNP (Craighead and Mindel1 1981; Craighead et al. 1987*). During the first year of this study, 2002, I surveyed 137 km^2, but subsequently enlarged the study area for 2003 and 2004. Elevations in the mountain valley range from 1900 to 2350 m, with the Teton Range to the west and Gros Ventre Range to the east. The Yellowstone National Park plateau lies to the north and the town of Jackson, Wyoming, is located to the south, where the two mountain ranges converge. The valley contains the Snake River corridor and an isolated, forested butte. From the European settlement of Jackson Hole until the valley was established as a National Park in 1950, hayfields and grazing accounted for most of the agricultural practices with the study area. By transferring cultivated field locations from old photographs (ca. 1960) into ArcView 3.3 (ESRI Inc., Redlands, CA), I determined that approximately 3100 ha were cultivated hayfields until the 1950s, and these areas have since reverted to fallow and sagebrush (*Artemisia tridentata*) fields. Presently, only 110 ha are being hayed with cattle present and grazing at various times of the summer months. Also, bison, antelope, deer, and moose graze the valley floor. Wolves, elk, black (*Ursus americanus*) and grizzly bears (*U. horribilis*), and cougars often use areas on the butte, river bottoms, forest tracts, and intermittently in the sage flats throughout the year. The winters are long and cold (late September - early April; mean daily temperature = -8.6°C), and the summers are short and cool (late April – early September; mean daily temperature = 24.4°C). Most of the yearly precipitation is in the form of snow (annual mean snowfall = 4.9 m).

The vegetation in and around the study area was originally described by Craighead and Craighead (1956). Sagebrush/bitterbrush (*Artemisia tridentata* and *A.*

arbuscula/Purshia tridentata) with stands of aspen (*Populus tremuloides*) dominate the valley floor. Fallow fields consist mostly of brome grass (*Bromus* spp.) with alfalfa (*Medicago sativa*) intermixed. The butte consists mainly of lodgepole pine (*Pinus contorta*), Engelman spruce (*Picea engelmannii*), blue spruce, (*picea pungens*) and Douglas-fir (*Pseudotsuga menziesii*), and the riparian areas are dominated by willow (*Salix* spp.) and cottonwoods (*Populus angustifolia* and *P. balsamifera*).

Survey techniques and productivity estimates

I began nest searching in May for the 2002 and 2003 study seasons, and April in 2004. Historical nest sites were checked first to determine if they were reoccupied, and then systematic searches of all suitable habitats were performed on foot to locate other occupied nests. I walked all forest and riparian areas to survey for nest structures and kept track logs using GPS recievers (Garmin, Olathe, KS). The tracks were then loaded onto ArcView 3.3 and any area that was not surveyed to within 100 m of the nearest track was visited and searched. Open areas were surveyed from a distance using binoculars or spotting scopes. On steep slopes or in areas easily observed from an area of higher elevation, I watched from a distance for any raven activity, and followed up with foot searches for nests following Craighead and Craighead (1956). Also, any recurrent raven activity that was observed in or around any area with trees was resurveyed for occupied nests if none were found during initial searches. Only the nests in the Craighead study area were used in the analysis of historical productivity to provide for a consistent comparison. To assess overall nesting density and to compare estimates with the literature, all nests found in the entire study area were analyzed.

To estimate the approximate egg laying date, I monitored adult behavior, climbed to nests, or used a mirror pole (Parker 1972) to inspect nests visually when observation from a distance was impaired. To minimize the potential for nest disturbance, I monitored the nests from >100 m if I had suspected that egg laying had occurred within the previous two weeks based on adult behavior. All eggs were counted when I climbed to a nest or used a mirror pole.

After banding (~18 days post-hatching), young in nests were monitored every 1-2 days to determine fledging dates and to quantify the number of fledglings. I obtained visual confirmation of nestling survival whenever possible for all banded young during this period.

Density Estimates

Data from 2002 was not included in density estimates because the study area was not expanded beyond the Craighead study area in 2002 until later in the breeding season, so there was a reasonable probability that I missed nests that had failed early that year. For estimates of fledglings/successful nest, I used data from all nests found within the study area, because all nests sampled were found before fledging. I calculated density estimates in three different ways to allow comparisons with previous raven studies. I first calculated density simply by dividing the number of breeding pairs present by the study area. I considered a pair as actively breeding if they displayed nest defense and courtship behavior. In all but one case, I found a nest that corresponded to the presence of a pair. In the one exception, I observed unbanded fledglings later in that territory being fed by the adults, indicating that I missed an occupied nest.

Second, I calculated density by using nearest-neighbor analysis. This analysis may be a more appropriate estimate of nesting density, as it alleviates the issues associated with habitat heterogeneity and arbitrary study area boundaries (Ratcliffe 1997). I plotted all nests in ArcView 3.3 and measured the nearest neighbor distance (NND). I corrected for GPS location error by plotting nests to the exact tree using 2002 aerial photographs.

Finally, for 2003 and 2004 data, I devised an alternative method, the “proximate nesting density,” of estimating nest density to eliminate any errors or biases associated with an arbitrary study area boundary. The assign proximity function in ArcView 3.3 (Analysis Pak) assigns potential use area perimeters around each nest by drawing a boundary line half way between each neighboring pair of nests (Figure 2.2). By using this, I can estimate the areas around the outside edge of the study area boundary where nests may occur, but not located. I eliminated nests that lacked a neighbor on at least one side of its perimeter, and nests with use areas that extended beyond the study area, and then calculated the nesting density of the remaining territories (Figure 2.2). In this way, the core use areas of each pair delineate the area to be included in the density estimate, and estimates are not deflated by pairs that may have been overlooked because they were outside of the study area. Nesting attempts were considered re-nests if a pair failed and another nest within 1 km of the failed nest became occupied.

Statistical Analysis

I used linear regression to examine relationships between nesting density and productivity with year, visitor use in GTNP, hunter success from GTNP and the National Elk Refuge, and bison herd population numbers. Visitor use data were obtained from the

National Park Service Public Use Statistics Office (www2.nature.nps.gov/stats/). I obtained annual bison herd count and hunter success data from the Resource Management Office of GTNP. I also obtained hunter success data from the National Elk Refuge (B. Smith, pers. comm.), which comprises approximately 10,000 ha adjacent to the southern boundary of the study area. Because data were collected inconsistently throughout the decades, I had to test each variable separately when using the 1940s data. I used a best subsets regression for all factors with data from the 1970s to the present to look for trends. For the analyses on density, I used only density estimates for the Craighead study area for comparisons across years. For productivity comparisons, I compiled data from all past studies in the area.

I examined if the number of fledglings produced across years from a given territory tends to be constant, which may indicate unchanged territory or parental quality. To do this, I first generated a standard deviation and mean of the number of fledglings produced from all broods for which I had fledging data from 2002-2004. From this estimate, I calculated a stochastic brood size and standard deviation based on the distribution of brood sizes observed in the population (0-5 fledglings produced in a year). Then, I compared this estimated deviation in brood size to the actual deviation in annual brood sizes for each territory. If the actual deviation was smaller than the expected deviation, this indicated that the productivity of a given territory was relatively constant and did not fluctuate in a random manor. I tested the assumption that actual deviations were smaller than the expected deviations with a two sample *t*-test.

To examine the relative amount of potentially available food resources during the winter months; I used elk harvest estimates for the fall/winter prior to breeding to test for relationships between winter food availability and nest success (assuming that the same proportion of successful hunters left a *grolloch*). Using linear regression models, I related available *grollochs* with subsequent nesting density and fledgling numbers (dependant variables). I also tested for associations between all explanatory variables and nesting density without the 1940s data because the nesting density has appeared to remain relatively stable after the 1975 nesting survey.

I tested the variation among mean fledging dates across years by using the first fledging event (if nest mates fledged on different dates) as the fledging date for a given nest. I then calculated the mean fledging date for each year (2002-2004), and tested for differences with a Kruskall-Wallace test.

Results

Nesting Density

For the 3-yr period of study, I documented a total of 94 nesting attempts by ravens in Jackson Hole. Twenty-six of these attempts occurred in 2002, 33 in 2003 (one of which was a re-nesting attempt), and 35 nesting attempts in 2004 (including one re-nest). Density estimates for the entire study area were 1.9, 1.8, and 1.9 pairs/10 km^2 for 2002-2004, respectively. When the years were combined, there was a pooled density of 1.9 pairs/10 km^2 (1 pair/5.3 km^2; Table 2.1). The density estimate for the Craighead study area, which included a lower proportion of unsuitable habitat for ravens than the entire study area, was 3.43 pairs/10 km^2 for all years.

Using the assign proximity function in ArcView to estimate the use areas associated with each raven territory, I found that the “proximate nesting density” was 1 pair/3.68 km^2 and 1 pair/3.89 km^2 for 2003 and 2004, respectively. Collectively, with this technique, the mean nesting density is 1 pair/3.79 km^2, a less conservative estimate than 1 pair/5.32 km^2 determined by dividing nests found by study area. This technique produced a lower estimate for the Craighead study area (1 pair/3.17 km^2). In 2003, I found a mean nearest neighbor distance of 1.34 km (S.E. = 0.12, range = 0.59 – 3.04 km), and 1.45 km in 2004 (S.E. = 0.07, range = 0.97 – 2.53 km; Mann-Whitney U between years, P = 0.155).

Nesting density of ravens has been documented in the Craighead study area for three different decades, beginning in the 1940s (Table 2.1). There were significantly fewer nests in the 1940s than any other decade (F = 17.8; P = 0.003; Table 2.1).

The territory re-occupancy frequency from 2002 to 2003 was 81.5% (n = 27 territories). This was based on my assumption that nests located within 1 km of the previous year's nest location were within the same nesting territory. Limited data suggest this was a valid assumption. In 2003, I had marked three breeding adults from different territories and these all returned to the same territories (range = 0.15 - 0.64 km from the previous nest) in 2004. The reuse rate from 2003 to 2004 was 83.3% (n =30). Of the 25 territories that were located in 2002 and rechecked in 2004, 80% were re-occupied (Table 2.2).

Within the Craighead study area, two of the three territories found in 1947 were reoccupied in 2004, and eight of ten territories found in 1987 were reused during the current study (Table 2.2). Unfortunately, maps delineating nest locations in the 1970s were lost in a fire (D. Craighead, pers. comm.), thus analysis of nest site reuse from that decade was not possible.

I found that the nesting density of the Craighead study area was significantly related to year, (r^2 = 0.77, P = 0.001, n = 9). Likewise, density was positively related to visitor use of Grand Teton National Park (entrance gate numbers; r^2 = 0.64, P = 0.01, n = 9, Figure 2.3). However, year was also positively related to park visitation during this time period ($P < 0.001$).

I also found bison herd counts were not related to nesting density of ravens (r^2 = 0.34, P = 0.132, n = 9). Likewise, using data from Grand Teton National Park and the National Elk Refuge, I found that nesting density was not associated with the number of elk harvested in the previous fall/winter (r^2 = 0.40, P = 0.145, n = 8). Based on regression analysis, I found no model that showed a significant relationship between nesting density and any explanatory variable examined when data from the 1940s were excluded.

Because ravens do not mature sexually until at least 3 yr of age (Dorn 1972*; Davies and Davies 1986), there may be a 3-yr, or longer, lag following a year with abundant food resources to an increase in breeding ravens. Using this logic, I predicted that the density of ravens should correlate with elk harvests from 3 yr prior because of enhanced survival the year after the birds fledge. With this lag time, I found that nesting density was positively related to elk harvest three years prior (r^2 = 0.78, P = 0.004, n = 8; Figure 4).

Productivity

From a total of 80 nests monitored in all three years, I found that 85.7% of all nesting pairs produced nestlings (2002 = 83.3%; n = 10, 2003 = 88%, n = 35; 2004 = 86%, n =35). I found that most mortality occurred during the nestling period, with only

37% of all nesting pairs producing fledglings (2002 = 26%, 2003 = 48%, and 2004 = 46%). In 2003, 17 successful pairs produced 47 fledglings, or 3.13 fledglings/successful pair. I recorded 37 fledglings in 2004, or 2.31 fledglings/successful pair (*n* = 16 nests). This was similar to data 2002 in which I found 17 fledglings, or 2.00 fledglings/ successful pair (*n* = 7 nests; Table 2.3). I found no statistical differences between years (P = 0.340). The mean for all years is 2.48 fledglings/successful pair (*n* = 40).

The annual reproductive success was 0.77 and 1.53 fledglings/occupied nest (total number fledged/total number of nests with eggs; range = 0-5) in 2002 and 2003, respectively. In 2004, I found the annual reproductive success to be 1.12 fledglings/ occupied nest (range = 0-5, *n* = 33). The mean for all years was 1.14 fledglings/nest (*n* = 92 fledglings). There was no difference among years for the number of fledglings from each nest (P = 0.710).

Of the 14 territories for which I have fledging data for all three years, I found that they collectively produced fledgling numbers that varied less than expected (P = 0.001), indicating the population may be producing a consistent number of fledglings. When I separated each territory and tested the differences between the standard and expected deviations for the three years, I found four territories that varied less than expected ($P < 0.05$, Table 2.4).

Using linear regression, I found that the elk harvested in the previous fall/winter in GTNP and the NER, combined, was not related to nest success. Also, productivity was not related to year or raven nesting density (P = 0.363 and 0.298, *n* = 10 and 6, respectively). However, nest success was negatively related to the number of bison present in the GTNP herd ($r^2 = 0.54$, P = 0.015).

The mean fledgling date (based on the first fledgling leaving the nest) for 2002 was 23 June (S.D. = +/- 6 days), 2003 was 15 June (S.D. = +/- 4.63 days), and 2004 was 15 June (S.D. = +/- 4.5 days). I found that that the mean fledging date for 2002 was later than fledging dates for 2003 and 2004 ($Z = 3.53$, $P = 0.002$). There was no difference in fledging dates between 2003 and 2004.

Discussion

Nesting Density

The density of Common Ravens in Grand Teton National Park is among the highest densities recorded in the literature (Table 2.5). This was surprising, considering ravens were not documented in Jackson Hole until 1938 (Stegner 1963). Based on the data available (Table 2.1), I suggest that most of the population growth occurred between the mid-1940s and the early 1970s, because the population has remained relatively stable after 1975 (Table 2.1). I further propose that because of the relatively stable population after a period of probable rapid growth, that the population is fluctuating around carrying capacity.

Dunk et al. (1994) reported that the density of nesting ravens in Jackson Hole was 0.73 nests/km^2, and that this was the highest raven density reported in the literature. However, they only surveyed 13.1 km^2, and did not include any non-suitable habitat by defining their study area in an irregular and non-contiguous pattern configured around suitable nesting habitat. Later, Craighead and Mindell (1981) reported densities as high as 0.35 nests/km^2 for this area. Again, their study area was relatively small (31.1 km^2), but did include some intermixed patches of unsuitable habitat. Bednarz et al. (1990)

caution about post-hoc delineating of small study areas around identified nests for measures of nesting density, and my data supports their concern that this procedure may inflate estimates of nesting density. While the Craighead study area remains small (31.1 km^2), multiple-year surveys indicate that the population of ravens has remained relatively constant since 1975. My density estimate of 0.18 nests/km^2 within the 181 km^2 study area may be more indicative of the true population density of this area. This estimate still remains higher than the density of nesting ravens reported for other locations in Europe, and represents the second highest density reported in North America, following a population in Camp Pendleton, CA (Linz et al. 1992; Table 2.5). Linz et al. (1992) found that this high population density surrounded a California Least Tern (*Sterna antilarum*) colony, but offered no speculations on factors that may be responsible for supporting such a high density.

Nearest neighbor analysis may be a more accurate technique of characterizing population densities because it reduces biases related to using variable size and shape sample plots (Clark and Evans 1954). By using mean nearest neighbor distances, habitat heterogeneity is taken into account. However, only three previous North American studies on ravens have adopted this approach for comparing raven populations, and one was of the same population that I have investigated in Jackson Hole (Hooper et al. 1975; Steenhof et al. 1993; Dunk et al. 1994). While Dunk et al. (1994) calculated density of this raven population at 0.73 pairs/km^2 and I found density at 0.18 pairs/km^2 based on the plot approach; the mean nearest neighbor distance was similar for both studies (Dunk et al. 1994 = 1.6 km, this study = 1.4 km). This comparison supports the use of the use of nearest neighbor analysis to characterize densities when study areas are small. Steenhof et al. (1993) found the nearest neighbor distance (NND) for ravens nesting on a 596 km stretch of transmission line towers to be 0.3 km, indicating a much higher linear density. However, there was no natural nesting substrate within 1-5 km of the line (Steenhof et al. 1993), which may have concentrated nests in a linear fashion because of limited suitable nesting substrate in the surrounding habitat.

Population Limitation

There was a positive relationship between nesting density and year, beginning in 1947. Two raven inventories in 1947 and 1948 demonstrate low densities, while the density was high and stable since 1975. Such stability is characteristic of larger, territorial birds, such as birds of prey, which fluctuate as little as +/- 15% of the mean across decades (Newton 1979, 1998). Also, population stability normally occurs in stable environments (Newton 1998). Therefore, some environmental factor during the 1930s through the 1970s likely have changed, and likely caused a response in raven population dynamics. Considering that the population has remained relatively stable since the 1970s, I suggest that some unknown, limiting population factor has been reached.

I have found some anecdotal evidence that breeding spaces may be limited in the Wyoming study area. I have documented that a marked male who lost his mate during incubation, procured a new mate and this pair began re-nesting in a new location within 2 wk. This observation suggested that breeding vacancies were limited and there was a surplus of non-breeding birds waiting for territory openings (Knapton and Krebs 1974). The availability of additional mature, but non-breeding birds was further supported by the presence of large, gregarious flocks of ravens that occur throughout the study area during the summer (Dorn 1972*; pers. obs. of flocks with ~ 20 nonbreeding ravens). The presence of these flocks, again, suggested that there were surplus ravens that cannot secure suitable nesting territories.

I found that raven nesting density was associated with the number of elk harvested in the fall/winter after a 3 yr lag period (Figure 2.4). Likewise, there was a significant relationship between harvest rates and year (White 2002*). If the key factor for increasing nesting density is winter food availability, and elk *grallochs* seem to be contributing to the availability of food, then ravens should have always utilized this resource. Because elk have been harvested within the valley from the time of white settlement of the area (Merriam 1873*), it raises the question “why did the ravens not occur as well?” Ravens were not reported in the area until the 1930s (Fuller and Bole 1930*), well after elk harvesting began. Likewise, the number of elk harvested has been constantly increasing since the 1930s (Wyoming Game and Fish, unpubl. data), which does not directly reflect the pattern exhibited by ravens, which plateaued between 1948 and 1975.

In North America, high raven density has been reported to be a product of human augmentation of the landscape or food resources (Knight 1984; Knight and Kawashima 1993; Steenhof et al. 1993; Webb et al. 2004; Roth et al. 2004), in which humans provide more nesting structures (e.g., power poles) or food (e.g., landfills). However, Nogles (1994) did not consider humans a factor in supporting a very dense population of ravens in the Canary Islands (Table 2.5). He suggested that a lack of carrion-eating competitors and an abundance of nest sites were important to the high density found in this population.

For the Jackson Hole ravens, Craighead and Mindell (1981) suggested that increasing human settlements in the Craighead study area may have caused the increase in ravens. However, there are fewer anthropogenic resources now than there were in previous decades, while raven population numbers have changed very little. Dorn (1972)* reported heavy use of three landfills by ravens within GTNP in 1971 and 1972, but these landfills were dismantled and covered in the 1980s (D. Craighead, pers. comm.). If ravens depended on such a human subsidy as suggested by Knight (1984), Knight and Kawashima (1993), and Webb et al. (2004), then I surmise that the raven population should have declined after the closure of these sites. This decrease did not occur, suggesting that the ravens had adequate food resources without the presence of these landfills. Conversely, I did find a positive relationship between nesting density and park visitation rates (Table 2.3).

Ravens are thought to be subsidized predators that take advantage of subsidies from large carnivores when present (Stahler et al. 2002; White 2002*; Vuetich et al. 2004). Alternatively, humans are often a source of subsidies during the winter months for ravens, usually by providing refuse, *grallochs*, and vehicle-killed animals (Dorn 1972*; Ratcliffe 1997; Boarman and Heinrich 1999; White 2005). When I tested the association between nesting density of ravens and elk harvest (index of available *grallochs*), I found no relationship between harvest and density the following spring. However, upon doing a post-hoc analysis, I found that there appeared to be a 3 yr lag time in the response of nesting density to increased elk hunting. In the winter of a good hunt year, there may be increased fitness, less dispersal, and increased survivorship of first-year ravens because food is more easily attained. Three years later, this larger than normal cohort will reach breeding age and try to obtain breeding spaces, therefore increasing the nesting density for that year (Figure 2.4).

Productivity

The reproductive success for this population of ravens is the lowest reported from North America (Table 2.4). While many studies have examined productivity of Common Ravens (Tables 3 and 6), few have examined the effects of environmental parameters on success. Dunk et al. (1997) found that in years with less cumulative snowfall, pairs nested earlier. They also found that clutch size was greater in the year with less snowfall, but they did not directly test the influences of weather on productivity (pairs producing fledglings). I found no differences in the number of fledglings produced between 2002-2004, even though ravens nested significantly later in 2002. Several authors have reported that in years when songbird pairs nested early, they had greater success at fledging young (Perrins 1970; Parsons 1975; Spear and Nur 1994),

The only variable I found associated with productivity was the size of the bison herd. This association was negative, with decreased productivity following an increase in herd size. This appears counterintuitive because of the long-standing association of ravens and bison (Houston 1977) and because of the fact that ravens often use bison chips as a food resource by flipping and feeding on insects found underneath the chips (Heinrich 1989; pers. obs.). Land use practices have reverted from irrigated agriculture back to natural fields during the years of bison herd expansion (D. Craighead, pers comm.), which complicates this association. Further, the bison herd began to increase

(GTNP, unpubl. data) after I suspect the ravens had reached carrying capacity, which may be a better explanation for decreased reproductive success.

Newton (1979) suggested that breeding on the same, suitable, territory across years may be beneficial because birds may be more successful in areas with which they are familiar. Dorn (1972*) and Boarman and Heinrich (1999) noted that some ravens attempt to maintain breeding territories year-round, suggesting that there may be some advantage to defending and reusing specific territories. However, Ratcliffe (1997) suggested that in ravens, territories may not differ in food-resource quality because of their large, overlapping, feeding areas. If this is the case, differences in productivity between nests may be primarily related to parental abilities. Although I could not differentiate between parental abilities and territory quality, my data suggested there was relatively low variation in productivity within each nest territory over time compared to the distribution of brood sizes observed (Table 2.4). Long-term data with marked individuals and productivity are needed to understand these effects of parental abilities and territory quality.

Population Ecology

While the cause of the increase of Common Ravens in Jackson Hole stills remains unknown, the population has remained remarkably stable for at least 35 yr. I suggest that possibly prior to the 1970s, relatively few people were residents and too few elk were harvested to support a persistent population of large, avian scavengers. According to the national census (www.census.gov/population/cencounts/wy190090.txt), less than 3100 people were residents of Teton County prior to 1960, but 4823 people were living in the county in 1970 (56% increase). Likewise, less than 325 elk were harvested annually before 1960 (range = 0-325, mean = 171.55) in the National Elk Refuge and Grand Teton National Park, combined, but up to 990 elk were harvested annually between 1964 and 1975 (range = 270-990, mean = 636.25). Also, the elk traditionally migrated out of Jackson Hole to the south (Cole 1969*). Because historical winter ranges could no longer be reached, the National Elk Refuge was formed to feed the elk supplementally in the winter, which resulted in increased herd size and hunter success in subsequent years (Bruce Smith, National Elk Refuge, pers. comm.). I suggest that when a critical threshold in available carrion was achieved, the area became more suitable for ravens. Since then, other avian scavengers have also colonized this area. American Crows (*Corvus brachyrhynchos*) were documented breeding in 1975 for the first time (Craighead and Mindell 1981). Bald Eagles (*Haliaeetus leucocephalus*) and Golden Eagles (*H. albicilla*) have increased dramatically in winter abundance during the fall months over the past 40 yr as a response to the elk harvest (D. Craighead, pers. comm.). Also, the first record of a breeding Turkey Vulture (*Cathartes aura)* in Jackson Hole occurred in 2004 (Cerovski et al. 2004*).

Given that I found a mean of 1.8 raven pairs/10 km^2 and a productivity of 1.33 fledglings/pair, the study area of 181 km^2 should produce an estimated mean of 43.57 fledglings/year. Of those fledglings, based on data from Ratcliffe (1997), approximately 52% will survive the first year, 70% the second year, and 80% the third year. That would leave only 12.68 recruits alive by the third year to enter the breeding population; assuming no emigration. Thus, each pair would have to reproduce an average of 5.37 years to replace themselves. This population projection is based on the assumption that bird can find a breeding vacancy at 3 yr of age, which may not be the case in a saturated population. Assuming it could take an extra year to procure a breeding territory; a bird that reproduces must live at least for 9 yr, and breed for an average period of 5 yr to maintain this population. Thus, the annual survival of the adults after the onset of breeding must be 88% for replacement to occur, which is a likely possibility. Because the population may likely produce more recruits than necessary for replacement, this would suggest that the Jackson Hole population of ravens may likely be a source population.

Ratcliffe (1997) estimated that in Europe, annual productivity should be at least 1.66 young/pair to result in a stable population. Productivity in the Jackson Hole study area was below this threshold (1.33 young/pair). However, the productivity needed for replacement in Jackson Hole may be below the figure estimated by Ratcliffe if survival is greater than the European population he studied. In Europe, ravens were subject to human persecution, which was considered in Ratcliffe's estimate. Conversely, because Grand Teton National Park is a protected area, there is very little human persecution of ravens. This would result in a decreased mortality rate and reduced productivity rates needed for replacement.

Particular raven nesting territories have been constantly occupied over the past 55 yr (Table 2.2). This may be further evidence that the Jackson Hole area is favorable for breeding. Either one raven of a pair is replaced at a time (pers. obs), or non-breeders are actively aware and searching for territory vacancies. In both cases, the population has a limit of breeding spaces, but not breeders, suggesting a population at carrying capacity. Further, limited evidence suggest that even territories that consistently produce no young are always occupied (Table 2.4).

To summarize, the nesting density within GTNP is among the highest estimates in the world, while the current productivity is among the lowest (Tables 2.5 and 2.6). Human influence may have positively influenced the nesting density of ravens between 1947 and 2004 (Figure 2.3). However, productivity of ravens in Jackson Hole was relatively low during the past 3 yr. This pattern was been documented in American Crows, where areas of human occupation (campgrounds) attracted crows, but may have adversely affected their reproductive success because of the need for a larger home range (Neatherlin and Marzluff 2004). Likewise, the density/productivity pattern exhibited in Jackson Hole is similar to one of the densest populations in Europe which exhibits very low productivity (reported by Ellis *in* Ratcliffe 1997). I suggest that an increase in anthropogenic influences has facilitated the increase in nesting ravens until they reached carrying capacity in the Jackson Hole study area sometime between 1947 and 1975. Subsequently, this large population may have been governed by density dependant factors and have limited reproductive success.

Documents Cited (Marked * in text)

Cerovski, A. O., M. Grenier, B. Oakleaf, L. Van Fleet, and **S. Patla.** 2004. Atlas of birds, mammals, amphibians, and reptiles in Wyoming. Wyoming Game and Fish Department. Nongame Program, Lander. 206 pp.

Cole, G. F. 1969. The elk of Grand Teton and southern Yellowstone national parks. Grand Teton National Park Research Report. www.cr.nps.gov/history/online _books /fauna8/fauna.htm

Craighead, F. L., F. C. Craighead Jr., and **J. W. Tischendorf.** 1987. Stability of raptor communities over time. Craighead Environmental Research Institute, Moose, Wy.

Dorn, J. L. 1972. The Common Raven of Jackson Hole, Wyoming. M.S. thesis, University of Wyoming, Laramie.

Fuller, A. B. and **B. P. Bole, Jr**. 1930. Observations on some Wyoming birds. Scientific Publication; Cleveland Museum of Natural History 1: 37-80.

Merriam, C. H. 1873. Report on the mammals and birds of the expedition, Pp 661-715. *in* F.V. Hayden, 6th Ann. Rep. U.S. Geol. Surv. Of Territories. Govt. Printing Office, Washington, D.C.

Stegner, H. 1963. Grand Teton Nature Notes, 4:8.

Stiehl, R. B. 1978. Aspects of the ecology of the Common Raven in Harney Basin, Oregon. Ph.D. dissertation, Portland State University, Portland, OR.

White, C. 2002. Influences of elk management on the Common Raven population of Jackson Hole, Wyoming. Thesis. University of Montana.

Literature Cited

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology. 73:794-804.

Bednarz, J. C., T. Hayden, and **T. Fischer**. 1990. The raptor and raven community of the Los Medanos Area in southeastern New Mexico: A unique and significant resource. Ecosystem Management: Rare and Significant Habitats. IN: New York State Museum Bulletin 471: 92-101.

Boarman, W. I. and **B. Heinrich.** 1999. Common Raven (*Corvus corax*) *in* The Birds of North America, No 476 (A. Poole and F. Gill, eds.) The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Clark, P. J. and **F. C. Evans**. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445-453.

Craighead, J. J. and **F.C. Craighead, Jr.** 1956. Hawks, owls and wildlife. Stackpole, Harrisburg, Pennsylvania.

Craighead, F. C., Jr., and **D. Mindell.** 1981. Nesting raptors in western Wyoming, 1947 and 1975. Journal of Wildlife Management 45: 865-872.

Davies, P. E. and **J. E. Davies.** 1986. The breeding biology of a raven population in central Wales. Nature in Wales 3: 44-54.

Dunk, J. R., S. L. Cain, M. E. Reid, and **R. N. Smith.** 1994. A high breeding density of Common Ravens in northwestern Wyoming. Northwestern Naturalist 75: 70-73.

-------, R. N. Smith, and **S. L. Cain.** 1997. Nest-site selection and reproductive success in Common Ravens. Auk 114: 116-120.

Fernandez, C., P. Azkona, and **J. A. Donzar.** 1998. Density-dependant effects on productivity in the Griffon Vulture *Gyps fulvus*: the role of interference and habitat heterogeneity. Ibis 140: 64-69.

Heinrich, B. 1989. Ravens in winter. Cliff Street Books, New York.

Hooper, R.G., H. S. Crawford, D. R. Chamberlain, and **R. F. Harlow.** 1975. Nesting density of Common Ravens in the Ridge Valley region of Virginia. American Birds 29: 931- 935.

Houston, C. S. 1977. Changing patterns of *Corvidae* on the prairies. Blue Jay 35: 149-156.

Knapton, R. W. and **J. R. Krebs.** 1974. Settlement patterns, territory size, and breeding density in the Song Sparrow (*Melospiza melodia*). Canadian Journal of Zoology 52: 1413-1420.

Knight, R. L. 1984. Responses of nesting ravens to people in areas of different human densities. Condor 86: 345-346.

------- and **J. Kawashima.** 1993. Responses of ravens and Red-Tailed Hawk populations to linear right-of-ways. Journal of Wildlife Management 57: 266-271.

Korpimaki, E. 1988. Effects of territory quality on occupany, breeding performance and breeding dispersal in Tengmalm’s Owl. Journal of Animal Ecology 57: 169-178.

Linz, G. M., C. E. Knittle, and **R. E. Johnson**. 1992. Home range of breeding Common Ravens in coastal Southern California. Southwestern Naturalist 37: 199-202.

McClaren, E. L., P. L. Kennedy, and **S. R. Dewey.** 2002. Do some Northern Goshawk nest areas consistently fledge more young than others? Condor 104: 343-352.

Myers, J. P., P. G. Conners, and **F. A. Pitelka.** 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. Auk 96: 551-561.

Neatherlin, E. A. and **J. M. Marzluff.** 2004. Responses of American Crow populations to campgrounds in remote native forest landscapes. Journal of Wildlife Management 68: 708-718.

Newton, I. 1979. Population ecology of raptors. Berkhamsted, Poyser.

--------- 1991. Habitat variation and population regulation in Sparrowhawks, Ibis I33: 76-88.

--------- 1998. Population limitation in birds. Academic Press, NY.

Nogles, A. 1994. High density and breeding distribution patterns of a Raven (*Corvus corax*) population on an oceanic island (El Hierro, Canary Islands). Journal of Avian Biology 25: 80-84.

Parker, J. W. 1972. A mirror pole device for examining high nests. Bird-Banding 43: 216-218.

Parsons, J. 1975. Seasonal Variation in the breeding success of the herring gull: and experimental approach to pre-fledging success. Journal of Animal Ecology 44: 553-573.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 306-315.

Poole**, K. G.,** and **R. G. Bromley**. 1988. Interrelationships within a raptor guild in the central Canadian Arctic. Canadian Journal of Zoology 66: 2275-2282.

Ratcliffe, D. 1997. The raven. Academic Press, San Diego.

Restani, M., J. M. Marzluff, and **R. E. Yates**. 2001. Effects of anthropogenic food sources on movements, survival, and sociality of common ravens in the Arctic. Condor 103: 399-404

Roth, J. E., J. P. Kelly, W. J. Sydeman, and **M. A. Colwell.** 2004. Sex differences in space use of breeding Common Ravens in western Marin County, California. Condor 106: 529-539.

Smith, D. G. and **J. R. Murphy.** 1982. Nest site selection in raptor communities of the eastern Great Basin Desert. Great Basin Naturalist. 42: 395-404.

Spear, L. and **N. Nur.** 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. Journal of Animal Ecology 63: 283-298.

Steenhof, K., M. N. Kochert, and **J. A. Roppe.** 1993. Nesting by raptors and Common Ravens on electrical transmission towers. Journal of Wildlife Management 57: 271-281.

Vucetich, J. A., R. O. Peterson, and **T. A. Waite.** 2004. Raven scavenging favours group foraging in wolves. Animal Behaviour 67: 1117-1126.

Webb, W. C., W. I. Boarman, and **J. T. Rotenberry.** 2004. Common Raven juvenile survivorship in a human augmented landscape. Condor 106: 517-528.

Table 2.1. Raven nesting densities in Jackson Hole, Wyoming within a 31.1 km study area during four decades.

Years Surveyed	Number of Pairs	Density (nests/10 km^2)	Source
1947-48	3	1.0	Craighead and Craighead (1956)
1975	11	3.5	Craighead and Mindell (1981)
1978-79	9	2.9	Craighead and Mindell (1981)
1987	10	3.1	Craighead et al. (1987)
2003-04	11	3.5	This Study

Table 2.2. Percent of raven nesting territories of re-occupied in northwestern Wyoming (*n*). Percentages are based on the number of territories reported during the year of the first study identifying those territories. For example, of the three territories found in 1947, all three were occupied in 1948, and two were occupied in all successive surveys (first column).

	1947	1948	1987	2002	2003
1947	-				
1948	100 (3)	-			
1987	66.7 (2)	66.7 (2)	-		
2002	66.7 (2)	66.7 (2)	70.0 (7)	-	
2003	66.7 (2)	66.7 (2)	80.0 (8)	70.0 (9)	-
2004	66.7 (2)	66.7 (2)	80.0 (8)	61.5 (8)	80.0 (8)

Table 2.3. Common Raven breeding performance in Jackson Hole, Wyoming over a 57-year period (1947-2004).

Year	Occupied Territories	Pairs Laying Eggs (%)	Pairs with Young (%)	Pairs with Fledglings (%)	No. Fledglings	Mean Clutch Size (SD, *n*)	Fledglings/ Territorial Pair	Fledglings/ Successful Pair
1947	3	3 (100)	3 (100)	3 (100)		5.70	3.30	3.30
1970-71	-	24 (-)	18 (75)	14 (58)	40	5.40 (1.0, 18)	1.67	2.86
1975	11	- (-)	- (-)	7 (64)	15	5.50 (- , 6)	1.40	2.14
1987	10	- (-)	- (-)	8 (80)	-	-	-	-
1992	13	13 (100)	12 (92)	11 (85)	42	5.30 (1.0, 6)	3.23	3.81
1993	21	21 (100)	17 (81)	13 (62)	37	4.56 (1.2, 16)	1.76	2.85
1994	11	10 (91)	10 (91)	9 (82)	26	4.09 (1.3, 11)	2.36	2.89
2001	13	- (-)	- (-)	7 (54)	22	-	1.70	3.10
2002	24	- (-)	19 (79.2)	10 (42)	20	4.90 (1.3, 11)	0.77	2.00
2003	32	31 (97)	29 (88)	15[1] (50)	47	5.10 (0.7, 10)	1.47	3.13
2004	36	34 (94)	31 (86)	16 (44)	37	4.63 (2.0, 16)	1.03	2.31

[1] Based on 30 nests; two nests were not re-checked before fledging departure and were eliminated from this estimate.

Table 2.4. Expected and observed deviations in the number of fledglings produced from territories in 2002-2004. Expected deviation in number of fledglings produced was based on the probability distribution of the brood sizes found throughout the population.

Territory	2002	2003	2004	Expected Deviation	Observed Deviation	Sign Test
Barn	2	3	2	2.33	0.44[1]	-
BTP	0	0	3	1.00	1.33	+
Curlew	1	2	2	1.67	0.44	-
Ditch Bridge	2	0	0	0.67	0.89[1]	+
Gun Range	3	0	4	2.33	1.56	-
Hayfields	1	2	0	1.00	0.67	-
HWY 89	3	0	1	1.33	1.11	-
Knob	2	4	3	3.00	0.67	-
McCallister	0	3	0	1.00	1.33	+
McReynolds	2	0	0	0.67	0.89	+
Meadow	0	0	0	2.33	0.00[1]	-
SE Blacktail	1	2	1	1.33	0.44[1]	-
Shirley	0	2	2	1.33	0.89	-
W Blacktail	3	4	5	4.00	0.67[1]	-
MEAN	1.43	1.57	1.64	0.81	1.69[1]	

[1] Significant difference compared to expected deviation.

Table 2.5. Density of breeding Common Ravens reported throughout the world.

Location	km^2 Surveyed	Pairs	Density (pair/ 100 km^2)	Source
United Kingdom[1]				
Wales	315	50	15.8	Newton et al. (1982); Davis and Davis (1986)
Wales	475	52	11.0	Cross and Davis (1986)
Devon	520	55	10.5	Kaczanow (1997)
Waterford	95	10	10.5	McGrath (1997)
Shetland	1468	150	10.2	Ellis et al. (1994); Ewins et al. (1986)
SWales	399	40	10.0	Dixon (1997)
Snowdonia	926	88	9.5	Dare (1986)
Orkney	974	90	9.2	Booth (1979)
Ross of Mull	175	16	9.1	Haworth (1997)
Isle of Man	565	40	7.1	Cullen and Jennings (1986)
Wales	160	10	6.3	Newton et al. (1982); Davis and Davis (1986)
Lake District	1235	75	6.1	Home et al. (1997)
Mull	359	20	5.6	Haworth (1997)
Snowdonia	690	38	5.5	Ratcliffe (1997)

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Table 2.5. Continued	km^2	Pairs	Density	Source
Galloway & Carrick	627	29	4.6	Ratcliffe et al. (1997)
Wales	288	11	3.8	Simson (1966)
Migneint-Hiraethog	477	18	3.8	Dare (1986)
Argyll	1689	62	3.7	Thomas (1993)
Mull	583	19	3.3	Haworth (1997)
Moffat Hills	305	9	3	Ratcliffe (1997)
Ireland	2025	57	2.8	G. C. Noonan in Hutchinson (1989)
Perth-Stirling-Dunbarton	1910	35	1.8	Stirling-Aird et al. (1995)
Wester Ross	1115	18	1.6	Ratcliffe and Balharry (1997)
Connemara	1690	26	1.5	Haworth (1997)
Sutherland	1396	16	1.2	Ratcliffe and Rae (1997)
Cheviots	2040	11	0.5	Galloway and Meek (1983)
Pennines	3920	10	0.3	Ratcliffe (1960)[2]
Germany[1]				
Schleswig-Holstein	170	8	4.7	Simson (1966)
Mecklenburg	-	-	4.7	Prill (1982)
Germany	2280	-	0.7-2.1	Looft (1983)

Table 2.5 Continued	km^2	Pairs	Density	Source
Wolgast	107	20	18.7	Sellin (1987)
North America				
California	66	14	21.3	Linz et al. (1992)
Wyoming	**181**	**34**	**18.8**	**This Study**
Oregon	732.5	87	4.0-4.6	Stiehl (1978)*
Utah	207	4	1.9	Smith and Murphy (1982)
NW Territories	-	-	0.35-0.6	Poole and Bromley (1988)
Other Areas[2]				
Canary Islands	278	194	34.2-35.6	Nogales (1994)
Botosani, Romania	490	47	9.6	Andriescu and Corduneau (1972)
Tula Forest, Russia	-	-	7.5	Likhachev (1951)
EI Salvador	200	12	6	Dickey and Van Rossem (1938)
Granada, Spain	104	6	5.8	Zuniga et al. (1982)
Canary Islands	2036	75	3.4-3.9	Martin (1987)
Switzerland	2500	75	3.0	Oggier (1986)
Iceland	-	-	1.5-6.8	Skarphedinsson et al. (1990)

[1] Reported in Ratcliffe (1997).

[2] Reported in Nogles (1994).

Table 2.6. Nest success (nests with fledglings/nests with eggs) and mean fledglings per nest of Common Ravens in North America.

Location	Nest success (%)	Mean fledglings/nest	S.E.	range	*n*	Source
Idaho	47.7[1]	3.1	0.3	2.5-3.4[2]	104	Steehhof et al. 1993
Oregon	85	2.3	2.0	2.2-2.5[2]	53	Steihl 1978*
Utah	16	2.6	0.3	2.5-3.0[2]	14	Smith and Murphy 1982
Virginia	35	2.8	-	1-4	44	Hooper et al. 1975, Hooper 1977
Wyoming	24	1.7	1.6	0-4	24	Dorn 1972
Wyoming	70	2.4	1.9	0-6	41	Dunk et al. 1997
Wyoming	52	1.3	1.6	0-5	63	This Study

[1] Mean from seven years.

[2] Range across years.

Figure 2.1. Study areas. Diagram A shows the greater Yellowstone ecosystem (composed of six national forests, two National Parks, and a National Wildlife Refuge) and the study area is shaded. In view B, the entire study area is the outer polygon and the Craighead and Craighead (1956) study area is the inner rectangle.

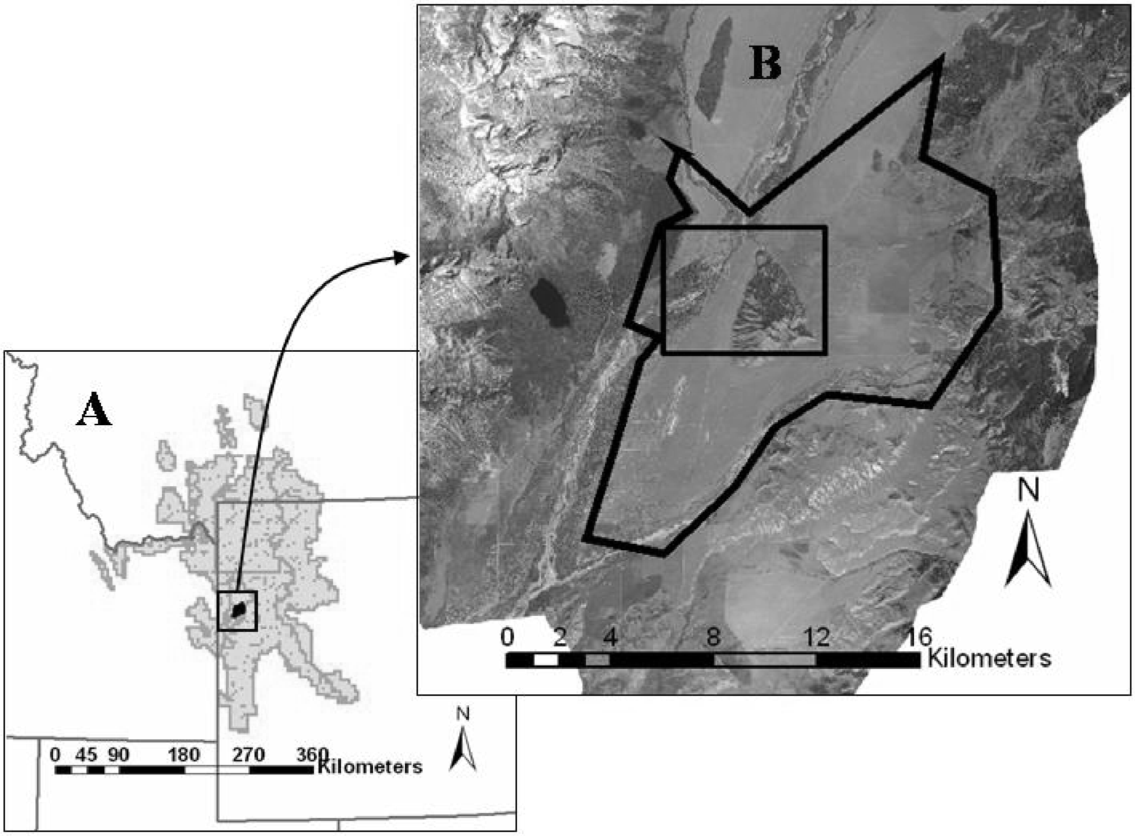


Figure 2.2. Grand Teton National Park raven nest density in 2004 estimated using the proximity to the nearest neighbor analysis. The outer polygon is the defined study area for 2004, and the inner polygon is the perimeter of the area used to compute the nesting density.

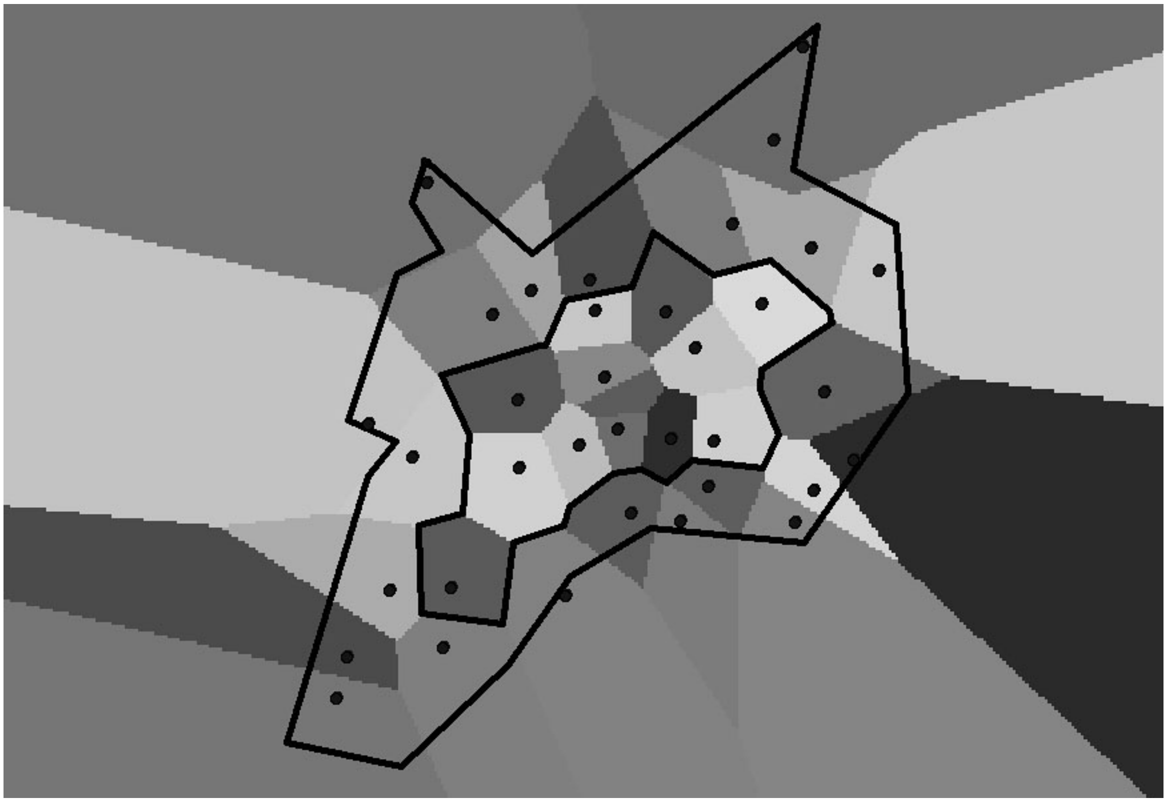


Figure 2.3. Patterns visitor use and number of Common Raven nesting pairs within a 31.1 km^2 study area within Grand Teton National Park for 57 years (1947-2004).

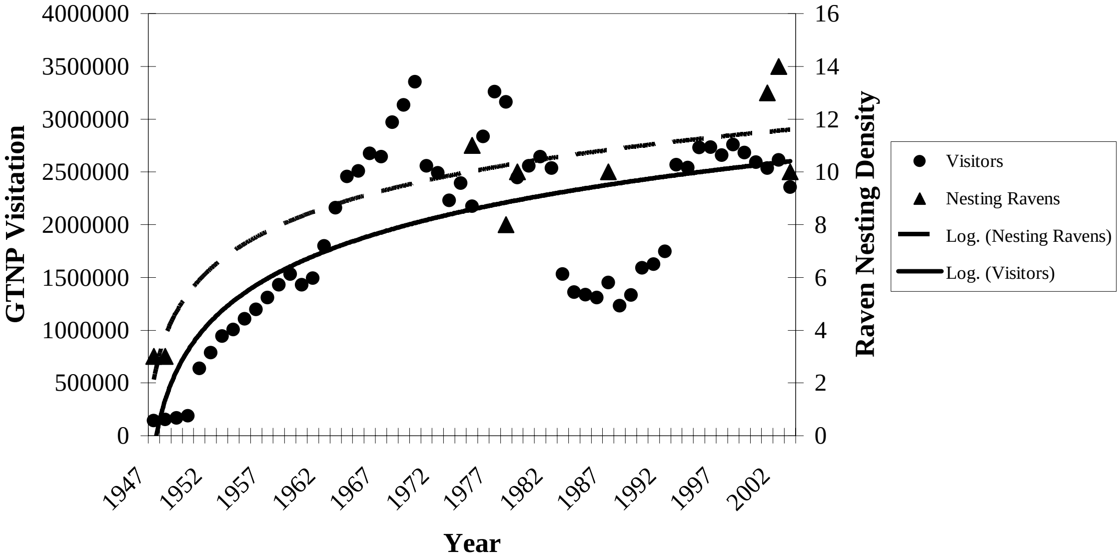
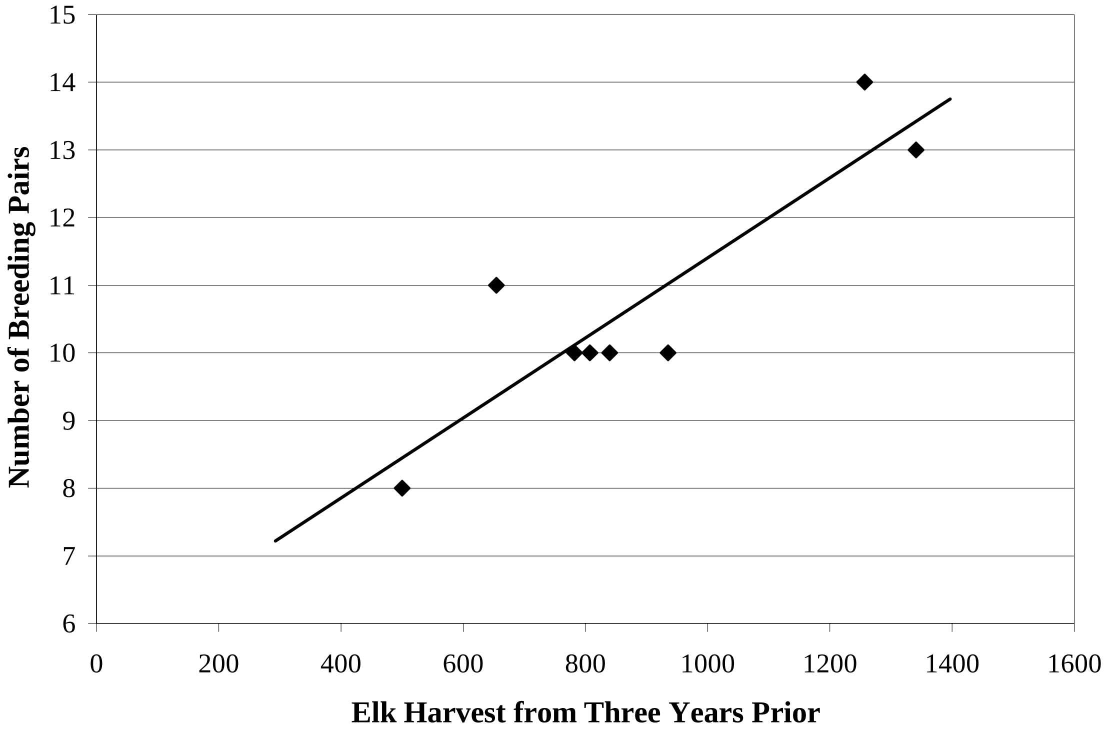


Figure 2.4. Relationship of territorial raven nesting pairs and elk harvest from three years prior to nesting surveys within Jackson Hole from 1975-2003 ($r^2 = 0.7818$).



Chapter 3

Post-fledging Mortality of Common Ravens:
The Proximate Causes and Potential Influencing Factors

Abstract

Factors influencing avian juvenile survival after fledging are much debated and may vary regionally for each species. Here, I present results on post-fledging mortality of Common Ravens (*Corvus corax*) in Grand Teton National Park (Jackson Hole), WY from 2003-2004. I found that 82.9% of juveniles survive to depart from their natal territories (*n* = 62 fledglings from 24 broods). Of the ten mortalities recorded, 60% were due to predation from coyotes (*Canis latrans*), red fox (*Vulpes vulpes*) and Great Horned Owls (*Bubo virgiananus*), 30% were caused by collisions resulting in traumas, and 10% were shot. I found that survivorship was not related to year, gender, distance between nests, distance to the nearest human-related food subsidy, brood size, or fledging date. In a similar study in California, Webb et al. (2004) reported a post-fledging survival rate of 38% in a human related food-augmented population of Common Ravens. My results demonstrated much higher survival for ravens in a population that was not noticeably augmented by humans. My results indicated that post-fledging survival within a species vary substantially, and therefore should be evaluated for each population separately.

Introduction

In order to assess population dynamics in birds, the breeding ecology of the involved species must be understood. While basic productivity studies are useful in comparing populations over time, resulting data may be of limited use in understanding the underlying causes of population dynamics if the ecology of mortality and dispersal of non-breeders are mostly unknown. Clutton-Brock (1988) suggested that in passerines, differential survival during the post-fledging period accounts for much of the variance in parental lifetime reproductive success. Therefore, to understand changes in populations of long-lived passerines, the patterns of post-fledging survival need to be understood. Factors that may contribute to mortality rates must be determined for populations under differing ecological pressures. This will not only provide more accurate estimates of recruitment and fitness, but such data in combination with information on the survivorship of the individuals and population density can be used to model population growth accurately.

Because of this interest in population dynamics and post-fledging ecology, there has been an increase in studies devoted to survival and recruitment of both juvenile and sub-adult birds during recent years (e.g., McFadzen and Marzluff 1996; Naef-Daenzer et al. 2001; Kershner et al. 2004; Webb et al. 2004). However, the post-fledging dependence period remains among the least-known periods of population demographics for most birds (Kershner et al. 2004). Of several studies that have investigated this critical period, few have obtained results that concur on the main factors influencing juvenile mortality. For example, some authors hypothesize that brood size is an influencing factor on juvenile mortality (Ewald and Rohwer 1982; Slagsvold 1984; Husby 1986; Seddon and Heezik 1991), while others suggest that post-fledging mortality is more related to parental abilities (Verhulst and Tinbergen 1991; Brinkohf et al. 1993; Spear and Nur 1994). Alternatively, Kenward et al. (1993) have shown that fledging date is the most influential factor on mortality in Northern Goshawks (*Accipiter gentilis*), in that nestlings that fledged earlier had increased survival. However, Hunt and Hunt (1976) found that a decreased nestling period was positively related juvenile survival in Glaucous-winged Gulls (*Larus glaucescens*), not fledging date. Finally, other factors such as human influence and proximity have also been shown to influence post-fledging mortality in Common Ravens (*Corvus corax*; Webb et al. 2004).

Of several studies on juvenile survivorship, only a few have involved passerines (Krementz et al. 1989; Magrath 1991; Husby and Slagsvold 1992; Kershner et al. 2004; Webb et al. 2004), and four of these used mark-recapture methods that may underestimate survival rates (Kershner et al. 2004). In small passerines, Krementz et al. (1989) and Magrath (1991) found that nestlings that were heavier showed improved survivorship during the post-fledging period. Likewise, Krementz et al. (1989) and Naef-Dazner et al. (2001) found that an earlier fledging date was related to increased fledgling survivorship. Webb et al. (2004) found no relationship of nestling mass with survivorship in Common Ravens in California.

Webb et al. (2004) investigated the post-fledging dependence period for Common Ravens in a population augmented for food by humans within the Mojave Desert of California. These researchers found two factors that were related to post-fledgling survival; fledging date and proximity to the nearest human food subsidy (e.g., landfills, houses, artificial wetlands). These authors surmised that the population they studied was supplemented by anthropogenic resources, but survival was negatively influenced by mortality risks associated with the human-dominated landscape. I conducted a study similar to Webb et al. (2004), but in an environment where the ravens are not subsidized by humans during the breeding season, which provides a comparison to the results reported by Webb et al. (2004).

I tested four hypotheses concerning different factors that may influence post-fledgling survival of Common Ravens in a semi-wilderness area:

1. With the greater the number of nestlings in a nest, an increase in mortality will occur due to increased competition among siblings for limited resources, and possibly, preferential allocation of food resources by parents (Slagsvold 1984; Husby 1986; Seddon and van Heezik 1991). Conversely, a smaller number of nestlings in a brood should be relatively well fed, and therefore beg less, which in turn may attract fewer predators (Ewald and Rohwer 1982; Slagsvold 1984). Due to a suspected increased competition among fledglings of larger broods, I predicted that nests with greater brood sizes will stay together as a family group for shorter durations. Also, I predicted that young within a brood will disperse at different times in larger broods (>3 fledglings) compared to smaller broods.
2. Survival of young should be related to the parents' ability to provide adequate care for offspring (Lack 1947; Verhulst and Tinbergen 1991; Brinkohf et al. 1993; Spear and Nur 1994). Often, more experienced breeders nest earlier, have larger clutch sizes, and experience higher reproductive success (e.g., Finney and Cooke 1978; Dow and Fredga 1984; Perrins and McClery 1985; Nol and Smith 1987). Based on that hypothesis, I predicted that post-fledging survivorship would be greater for earlier nests, because that parameter is an indirect indicator of parental abilities or experience.

3. Post-fledging mortality of individuals may be directly related to hatch order within a brood, because development and mass at fledging is directly related to hatch order (Haydock and Ligon 1986; McGrath 1991; Van der Jeugd and Larsson 1998). Therefore, the older nestlings are generally in better condition, and thus, may have a higher probability of survival than the younger nestlings in the brood (Krementz et al. 1989; Husby and Slagsvold 1992). Specifically, I predicted that older nestlings within a brood would experience higher survival than their younger nestmates during the post-fledging period.

4. Nest placement within the landscape will influence juvenile survival due to proximity to subsidies and hazards. Webb et al. (2004) found increased juvenile survivorship when nests were located within 1.5 km of the nearest human food subsidy. I predicted that nests located near human subsidies would experience increase juvenile survival. Conversely, I predicted that juveniles in nests closer to potential hazards (e.g., roads, Red-tailed Hawk (*Buteo jamecensis*) nests, and conspecific nests) would experience decreased survival.

To address these predictions, I radio tracked 62 fledglings from 24 broods in 2003 and 2004 until they dispersed from their natal territories. I located and monitored nests within Grand Teton National Park, Wyoming, which has little influence from humans. I was able to document brood size, body condition indices, hatch order, dispersal dates, and distance of the nest to the nearest human subsidy, raven nest, Red-tailed Hawk nest, and road to evaluate factors influencing juvenile survival in the Grand Teton system. I also evaluated gender as a potential influencing factor on survivorship to determine if there was differential survival of juvenile Common Ravens.

Methods

Study Area

The study area encompasses approximately 181 km^2 of a mountain valley in the southwest corner of Grand Teton National Park (GTNP), which is situated in northwest Wyoming (43º91'N, 110º40'W). Elevations of the mountain valley range from 1932 to 2343 m, with the Teton Range to the west and Gros Ventre Range to the east. To the north lies the Yellowstone National Park plateau and the town of Jackson, Wyoming (population ca. 8700) is located 8.8 km to the south of the point where the two mountain ranges converge. The study area contains the Snake River corridor and an isolated, forested butte.

Presently, bison (*Bison bison*) and antelope (*Antelocapra americana*) graze the valley floor. Wolves (*Canis lupis*), elk (*Cervus canadensis*), black bears (*Ursus americanus*) and grizzly bears (*Ursus horribilis*), and cougars (*Felix concolor*) often utilize areas on the butte, river bottoms, forest tracts, and intermittently, the sage flats throughout the year. The winters in the area are relatively long and cold (late Sept - early April; mean daily temp = -8.6°C), and the summers are short and cool (late April – early Sept; mean daily temp = 24.4°C). Most of the yearly accumulation of precipitation is in the form of snow (mean snowfall = 4.9 m).

The vegetation in and around the study area was originally described by Craighead and Craighead (1956), and has changed little since (Dunk et al. 1997). Sagebrush/bitterbrush (*Artemisia tridentata* and *A. arbuscula/Purshia tridentata*) with stands of aspen (*Populus tremuloides*) dominate the valley floor. Fallow fields consist mostly of brome grass (*Bromus* spp.) with alfalfa (*Medicago sativa*) intermixed. The butte consists mainly of lodgepole pine (*Pinus contorta*), Engelman spruce (*Picea engelmannii*), blue spruce (*picea pungens*), and Douglas-fir (*Pseudotsuga menziesii*). The riparian areas are dominated by willow (*Salix* spp.) and cottonwoods (*Populus angustifolia* and *P. balsamifera*).

Nest searching and banding

Nest searching began in May in 2003 and April in 2004. Historical nest sites (Craighead and Craighead 1956; Craighead and Mindell 1981; Craighead et al. 1987*) were checked first to determine reoccupancy rates, and then systematic searches of all suitable habitats were performed on foot for other occupied nests. I walked all forest and riparian areas systematically (transects approximately 200 m apart) throughout the study area to survey for nest structures, and open areas with scattered trees were surveyed from roads using binoculars or spotting scopes. On steep slopes or in areas easily observed from an area of higher elevation, I watched from a distance for any raven activity, and followed up with foot searches for nests (Craighead and Craighead 1956).

If a nest survived to banding age, >18 days post-hatching, I banded the young with aluminum United States Geological Survey numerical bands and green anodized aluminum number/letter bands (Acraft Sign and Nameplate Co., Edmonton, Alberta). I measured culmen length, bill width, toe-pad length, hallux nail length, tarsus length and width, wing chord, tail length, and maximum head width on all nestlings. I also measured the 7th primary feather of all nestlings to obtain relative hatch order within the brood (Bednarz and Hayden 1991). Two 50 ul blood samples were collected from the brachial vein of each nestling. One of the blood samples was placed in 1 ml lysis buffer (Longmire et al. 1988) for DNA isolation by DNeasy tissue kit (Qiagen, Hawthorne, CA), and the other was placed in solution for West Nile Virus testing provided by the Marshfield Clinic (Marshfield, WI). All nestlings were later assigned as male or female using PCR techniques (Fridolfsson and Ellegren 1999).

A 3.50 g transmitter (Holohil Systems LTD., Carp, Ontario) was placed on the right leg above the anodized band using a leather jesse. I cut the jesse in half before attachment and repaired it using a 10 mm cotton thread coated in wax to provide a breakaway system for the transmitter (Figure 3.1). Also, I covered the antennas using dual colored shrink tubing (3M, St. Paul, MN; i.e. yellow, green, red, black, and white) with unique patterns for each transmitter to allow for easy detection and identification of individuals from longer distances. All of the young in a nest were fitted with transmitters. If a nestling died before fledging, or shortly after fledging, the transmitter was removed, cleaned, and placed on another nestling from a different nest that had not yet fledged to increase sample size. All nestlings from all accessible nests (*n* = 24) received transmitters.

Radio tracking

After banding, nests were monitored every 1-2 days to determine fledging date and to make certain that the young had not died prior to fledging. I attempted to obtain visual confirmation of nestling survival for all banded young during this period. After the first raven had fledged from a nest, I monitored that nest every day until I determined that all of the nestlings had fledged and were flying well enough to perch in trees and evade mammalian predators (0-5 d post-fledging). From that time until shortly before the onset of natal dispersal, I obtained visual confirmation that each fledgling was alive every

2-3 days. If it appeared that the young ravens were getting close to departure from the natal area because they were spending more time in flight and flying distances greater than 1.5 km from the nest, I again documented locations by visual confirmation daily. Any fledgling flying more than 3 km away from the nest site without returning for 3 consecutive days was classified as departed successfully from its natal territory (Wyllie 1985). If a fledgling was observed to move more than 3 km from its nest site during the day, subsequent roost locations were obtained to confirm dispersal. A fledgling was only considered departed after it did not return to the nest site to roost, which was often several days after the bird spent daylight hours >3 km from its natal area. Daily locations of each fledgling were plotted on 2002 aerial photographs (GTNP) in ArcView GIS (Environmental Research Systems Institute Inc., Redlands, CA), so that distance from the nest could be measured. Each fledgling's location was identified related to the distance from landmarks in the field (e.g., roads, fences, specific trees, forest openings), which I later identified on the aerial photographs to plot the location.

I performed a gross examination in the field of any juvenile raven carcasses found to help assess cause of death. Orientation of the body, tracks around the kill site and any other clues were noted. I later performed detailed necropsies on all carcasses and tissue samples were analyzed by the Wyoming State Veterinary Lab (Laramie, WY) for infections, viruses, and diseases that may have influenced mortality.

Statistical analysis

I tested for associations with survivorship as the dependant variable (survival as forward selection) with gender, brood size at fledging, body condition index, year, and the distance of the nest to the nearest human settlement, road, Red-tailed Hawk nest, and other Common Raven nests using binomial logistic regression (Webb at al. 2004). I used the residuals from a tarsus length on mass regression as the body condition index (Webb et al. 2004). I also separated nests into two categories based on whether at least one fledgling from the brood died or not to determine if any of the measured factors could help predict between completely or partially successful broods. Further, I examined the influence of gender on survivorship by estimating survival probability distributions with the Kaplin-Meier (1958) method. Human settlements were considered anywhere humans were commonly and continually present throughout the breeding season. These places included houses, campgrounds, small towns (population >25 people), and an airport.

Results

A total of 62 fledglings for 2003 and 2004 (28 and 34, respectively) from 24 broods were fitted with radio transmitters and monitored for survival throughout the fledgling dependence period. I found that the mean post-fledging period was significantly shorter in 2003 than in 2004 (P = 0.002, 27.2 and 40.5 days, respectively). Five fledglings died each year, resulting in overall survival of 82% and 85% from fledging to juvenile departure for 2003 and 2004, respectively. Collectively, the survival rate of juvenile ravens prior to departure was 82.8 +/- 0.05% in Jackson Hole (Figure 3.2).

Of the ten mortalities recorded, 60% were due to predation, 30% were caused by collisions resulting in traumas, and the remaining 10% was related to human persecution (Table 3.1). Two fledgling ravens were determined to be killed by coyotes (*Canis* *latrans*) and both carcasses were discovered buried, but not eaten. Foxes (*Vulpes fulva*) were identified as predators in two deaths, and both of these carcasses were consumed. Two other predation events occurred, but both of the carcasses were entirely consumed and there was no evidence to suggest either mammalian or avian predators. I surmised that head traumas were probably the result of uncontrolled "crash" landings, causing the deaths of two fledglings. One fledgling died from starvation because it had a broken wing and could not follow its parents and beg for food. One fledgling was shot by a human. Most of the post-fledging mortalities (80%) occurred during the first week after fledging (Figure 3.2).

In 2003, I found that 49% of all nestlings that were sampled for gender were female (*n* = 22) and 51% were males (*n* = 23). In 2004, 54% of the nestlings sampled were females (*n* = 18), while 46% were males (*n* = 15). Collectively, the sex ratio for both years was 51:49 in favor of females.

The only factor examined that had some relationship with survivorship within the post-fledging dependence period was the distance to the nearest human settlements (Table 3.2; Goodman-Kruskal gamma score = 0.51). I found that the chance of survivorship increased by 66% if the nest was within 1 km from the nearest human settlement. Non-significant factors included gender, fledging date, condition index, hatch order, brood size at fledging, year, and distances to the nearest neighbor and road (Figure 3.3-9; Table 3.2).

Whether a brood was completely or partially successful was not dependant on fledging date, brood size at fledging, year, or the distance of the nest to the nearest neighbor, human settlement, and road (Table 3.3).

Discussion

I found very high survivorship in juvenile ravens prior to dispersal from their natal territories (82.8%), and that the majority of the mortalities occurred within one week of fledging (Figure 3.2). With such low mortality of the fledglings within this population of ravens, I was unable to find enough evidence to support any of the hypotheses that I tested relating to juvenile mortality factors. I found that gender, fledging dates, juvenile condition, and relative age of the fledglings had no bearing on survival. This indicated that survivorship of the fledglings in the study population was not limited by parental allocation of limited food resources as suggested by Slavsgold (1984); Husby (1986); and Seddon and van Heezik (1991). Likewise, the evidence I collected does not suggest that juvenile survivorship is related to parental care or breeding experience as suggested by Verhulst and Tinbergen (1991), Brinkohf et al. (1993), and Spear and Nur (1994) (Table 3.2). Kenward et al. (1993) and Webb et al. (2004) both suggested that an influential factor on juvenile survivorship is fledging date, but I found no evidence of such a relationship in the ravens of Jackson Hole (Table 2). Finally, I found no relationship between nestling age within a brood and survivorship, which indicated the hypothesis that hatch order is directly related to survivorship (Haydock and Ligon 1986; McGrath 1991; Van der Jeugd and Larsson 1998) did not seem to apply to this population.

The majority of the deaths in this population (90%; $n = 10$) were from natural causes, and there appeared to be minimal influences from humans that affect the survival of these birds. The major cause of death was from mammalian predators during the time period in which the fledglings had difficulty flying. During the first week out of the nest, I observed that most juveniles could not fly or were very inept at flight. The majority of the young spent most of their time on the ground or perched on a low log or fence during the first 1-5 days, which may make them vulnerable to mammalian predation. It is possible that raven nestlings cannot adequately exercise and build up flight muscles in the nest due to confined space in the nest. Therefore, a fledgling may need to fledge to build up adequate flight capabilities (0-5 days). However, by fledging prior to flight muscle development, the fledglings are at greater risk to predation by mammalian predators.

Post-fledging mortality of birds has been of interest since the 1970s, but most studies have used band recoveries and resightings to document survival. Even with the recent advances in radio-telemetry, there are few in-depth studies following specific individuals to initial dispersal from natal territories, and even fewer to first breeding. It is unknown how post-fledging survival estimates relate quantitatively to population demographics (Ganey et al. 1998), but fledgling survival is a fitness parameter that may be under strong selection pressure (Blums et al. 2002). Therefore, to document the spatial and temporal variation within a species, it is important to estimate survival in systems with differing in selective pressures (Hoekman et al. 2004). Without such data, management of a species based on an estimate from one population may be misleading for different regions.

Recently, Webb et al. (2004) completed a study in which they followed fledgling Common Ravens throughout the post-fledging dependence period, but in a population that was augmented by food subsidies from humans. I collected similar data on Common Ravens in Jackson Hole, but this population received little to no food subsidies from humans during the breeding season. My findings provide a comparison with the work of

Webb et al. (2004). The post-fledging survival of Common Ravens during the dependence period in the Jackson Hole ecosystem was on the high end of survival estimates relative to other estimates from a variety of avian taxa, while the survival of fledgling ravens in the Mojave is low (Table 3.4). Webb et al. (2004) found that Common Raven post-fledging survival in the Mojave Desert was related positively to the distance that the nest was from the nearest point subsidy (permanent food or water sources). There are no permanent food sources within my study area and water is most likely not a key factor related to survival as in a desert environment, as suggested by Webb et al. (2004). I did find a weak pattern that raven post-fledging survival in Jackson Hole may be positively related to the nest distance from the nearest human settlement (Figure 3.3, Table 3.2), which may represent opportunistic point subsidy sites. I found evidence that suggested the nest distance to the nearest human settlement influenced mortality ($P = 0.061$), but my sample size was limited (10 mortalities). Further, nest distance to the nearest settlement was not related to the probability that a brood of fledglings would be completely successful to dispersal (Table 2.3). According to Webb et al. (2004), juvenile ravens in California experienced higher survivorship with increased proximity to human food subsidies. However, they also found a highly significant relationship between nest distance to the nearest human activity and an anthropogenic cause of death (e.g., car collision). They also suggested that the high number of coyote-caused mortalities in nests closer to human settlements may be indirectly attributable to a human augmented coyote population. Therefore, the fact that Webb et al. (2004) found increasing juvenile survivorship associated with an increase in nest proximity to anthropogenic sources is overshadowed by the overall low survivorship of the population caused mainly by human-related deaths.

Newton (1998) suggested that in species where competition mainly occurs during the breeding season, changes in demographic variables such as breeding performance will may be influenced by density dependant population regulation. In earlier estimates of raven productivity in Jackson Hole, Craighead and Craighead (1956) found low nesting density with a relatively high reproductive rate. However, the reproduction rate of ravens in 2003 and 2004 were among the lowest recorded for Common Ravens throughout the world, while density was among the highest estimates (Chapter 2). Therefore, as the population of ravens in Jackson Hole has increased, the reproductive output may have declined because of intraspecific competition during the breeding season, which may account for low productivity estimates of this population.

Cooch et al. (1998), Francis et al. (1992), and Williams et al. (1993) suggested that a population under density-dependant selection will exhibit lower clutch sizes, brood sizes, nestling survival, and juvenile survival to one year post-fledging. Dunk et al. (1997) found that the clutch size for this population of ravens is low for the species (Boarman and Heinrich 1999), and that this Wyoming population had the lowest recorded productivity (Chapter 2). While these demographics coincide with a population under density-dependant selection, the post-fledging survival does not. If the ravens of Jackson Hole experienced density-dependant selection prior to 1975, which led to a stable, high, population thereafter (Craighead and Craighead 1956; Craighead and Mindell 1981; Craighead et al. 1987*; Chapter 2), then the brood size and juvenile mortality rates may have stabilized at low levels that would maintain that population level. Because it would not be energetically efficient to produce a large number of fledglings that experience high mortality, I suggest that it could be adaptive for ravens to produce low clutch and brood sizes, and focus parental care in a manner to enhance juvenile survivorship. This may indicate that the population may have stabilized as a result of density-dependant selection, but may be maintained by allocating parental investment in a manor to maximize post-fledging survival. By reallocating investment in the production of fewer, higher quality young, the adults also may gain enhanced survival by limiting the stress on themselves by caring for larger broods that include young that may likely die.

An alternative, and not mutually exclusive, hypothesis to explain the low productivity and high juvenile survivorship within this population is bet hedging within a fluctuating environment (Zammuto and Miller 1985). This theory suggests that in areas of fluctuating environmental conditions, pairs may produce smaller brood sizes with increased juvenile survivorship to increase lifetime reproductive success. This theory maintains that pairs who produce larger broods may experience greater variability in reproductive success among years, and have an overall decreased lifetime reproductive success due to this variability (Zammuto and Miller 1985). Pairs that produce large broods will be more susceptible to mortality because of a high degree of investment into their young, which will likely not survive every year in a fluctuating environment. Conversely, pairs that put relative little energy into a few young that have the same, or better, chance of survival will likely live longer and be able to reproduce for more years, owing to greater lifetime reproductive success.

While my data on lifetime reproductive success in this population of ravens are limited, it appears that some predictions put forth by the bet hedging hypothesis may hold true for this population of ravens. I found low variance in reproductive success of the population as a whole (Chapter 2), very low juvenile mortality, and low variance in juvenile mortality between years (5 deaths each year). There is limited evidence from this population that pairs return to breed on the same territories across years. Of four individual breeders banded within my study area, all have returned for four consecutive breeding seasons (B. Bedrosian, unpubl. data). This also supports that survivorship in adults is high.

The markedly different survival estimates found by Webb et al. (2004) and myself support the notion that population demographics differ regionally, and multiple investigations for each species are needed to assess fledging-dependence period survival adequately. While Webb et al. (2004) found very low survival (38%) for Common Ravens; I found a very high survival (83%) for the same species. Webb et al. (2004) surmised that the "dramatic increase" of ravens in the western Mojave has been largely due to an increase in anthropogenic resources available to the ravens of the area. Netherlin and Marzluff (2004) found that while American Crow (*Corvus brachyrhynchos*) populations were concentrated around campgrounds on the Olympic Peninsula, they experienced decreased reproduction compared to crows nesting in exurban areas surrounding the campgrounds. I suggest that a similar pattern exists with Common Ravens; in that they are attracted to areas of anthropogenic augmentation, but experience decreased survivorship. Because of hazards involved for ravens in areas of high human habitation, these areas may be acting as sinks. My results suggest that areas of little human influence may support enhanced survival of fledglings, and therefore, may result in a substantial increase in the recruitment potential of a population and represent a stable, if not source, population. Areas of low human augmentation may be needed for the demographic health of ravens. Alternatively, it is possible that both the California (Webb et al. 2004) and the Jackson Hole populations are at carrying capacity, yet have differing reproductive strategies giving similar density results. While my study population appears to have high survival of a few young, the population studied by Webb et al. (2004) may have low survivorship of many young because of the mortality risks associated with humans. It may not cause the breeding pairs too much stress to produce many young in human-augmented areas because of abundant, constant food resources provided by humans. In either case, the markedly different results obtained by Webb et al. (2004) and myself clearly indicate that the variation in post-fledging mortality may be quite substantial and it is important to assess juvenile survivorship for different populations to implement suitable regional species management of most species.

Documents Cited (Marked * in text)

Craighead, F. L., F. C. Craighead Jr., and **J. W. Tischendorf.** 1987. Stability of raptor communities over time. Craighead Environmental Research Institute, Moose, Wy.

Literature Cited

Bednarz, J. C. and **T. J. Hayden**. 1991. Skewed brood sex ratio and sex-biased hatching sequence in Harris's hawks. American Naturalist 137:116-132

Blums, P., R. G. Clark, and **A. Mednis.** 2002. Patterns of reproductive efforts and success in birds: path analyses of long-term data from European ducks. Journal of Animal Ecology 71: 280-295

Boarman, W. I. and **B. Heinrich.** 1999. Common Raven (*Corvus corax*) *in* The Birds of North America, No 476 (A. Poole and F. Gill, eds.) The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Brinkhof, M. W. G., A. J. Cave, F. J. Hage, and **S. Verhulst.** 1993. Timing of reproduction and fledging success in the coot *Fulica atra*: evidence for a causal relationship. Journal of Animal Ecology 62: 577-587.

Bustamante, J. 1993. Post-fledging dependence period and development of flight and hunting behavior in the Red Kite (*Milvus milvus*). Bird Study 40: 181-188.

Clutton-Brock, T. H. 1988. Reproductive success: Studies of individual variation in contrasting breeding seasons. University of Chicago Press. Chicago.

Cooch, E.G., D. B. Lank, R. F. Rockwell, and **F. Cooke.** 1998. Long-term decline in fecundity in a Snow Goose population: evidence for density dependence? Journal of Animal Ecology 58: 711-726.

Craighead, F. C., Jr., and **D. Mindell.** 1981. Nesting raptors in western Wyoming, 1947 and 1975. Journal of Wildlife Management 45: 865-872.

Craighead, J. J., and **F. C. Craighead, Jr.** 1956. Hawks, owls and wildlife. Stackpole, Harrisburg, Pennsylvania.

Dow, H. and **S. Fredga.** 1984. Factors affecting reproductive output of the Goldeneye Duck *Bucephala clangula.* Journal of Animal Ecology 53: 697-692.

Dunk, J.R., R. N. Smith, and **S. L. Cain.** 1997. Nest-site selection and reproductive success in Common Ravens. Auk 114: 116-120.

Ewald, P. W. and **S. Rohwer**. 1982. Effects of supplementary feeding on timing of breeding, clutch size and polygny in Red-winged Blackbirds *Agelaius phoeniceus*. Journal of Animal Ecology 51: 429-450.

Finney, G. and **F. Cooke.** 1978. Reproductive habits in the snow goose: the influence of female age. Condor 80: 147-158.

Francis, C. M., M. H. Richards, F. Cooke, and **R. F. Rockwell.** 1992. Long-term changes in survival rates of Lesser Snow Geese. Ecology 73: 1346-1362.

Fridolfsson, A-K and **H. Ellgren.** 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Bioogy 30: 116-121.

Haydock, J. and **J. D. Ligon.** 1986. Brood reduction in the Chihuahuan Raven: and experimental study. Ecology 67: 1194-1205.

Hoekman, S. T., T.S. Gabor, R. Maher, H. P. Murkin, and **L. M. Armstrong.** 2004. Factors affecting survival of mallard ducklings in southern Ontario. Condor 106: 485-495.

Husby, M. 1986. On the adaptive value of brood reduction in birds: experiments with the magpie *Pica pica*. Journal of Animal Ecology 55: 75-83.

Husby, M. and **T. Slagsvold.** 1992. Post-fledging behaviour and survival in male and female Magpies *Pica pica*. Ornis Scandinavica 23: 483-490.

Hunt, G. L. Jr., and **M. W. Hunt.** 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57: 62-75.

Kaplin, E.L. and **P. Meier.** 1958. Nonparametric estimation from incomplete observations. Journal of American Statistical Association 53: 457-481.

Kershner, E. L., J. W. Walk, and **R. E. Warner.** 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*). Auk. 121: 1146-1154.

Kenward, R. E., V. Marcstrom, and **M. Karlbom.** 1993. Post-nesting behavior in goshawks, *Accipiter gentilis*: I. The causes of dispersal. Animal Behaviour 46: 365-370.

Konrad, P. M. and **D. S. Glimer**. 1986. Post fledging behavior of Ferruginous Hawks in North Dakota. Journal of Raptor Research. 20: 35-39.

Krementz, D.G., Nichols, J.D., and **J.E. Hines.** 1989. Postfledging survival of European Starlings. Ecology. 70:646-655.

Lack, D. 1947. The significance of clutch size. Ibis 89: 302-352.

Longmire, J. L., A.W. Lewis, N. C. Brown, J. M. Clark, M. D. Jones, L. J. Meinke,

J. Meyne, R. L. Ratcliff, F. A. Ray, R. P. Wagner, and **R. K. Moyzis.** 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. Genomic 2: 14-24.

Magrath, R.D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. Journal of Animal Ecology 60: 335-351.

Mcfadzen, M. E. and **J. M. Marzluff.** 1996. Mortality of Prairie Faclson during the fledging-dependence period. Condor 98:791-800.

Naef-Daenzer, B., W. Fritz, and **M. Nuber.** 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. Journal of Animal Ecology 70: 730-738.

Neatherlin, E.A. and **J. M. Marzluff.** 2004. Responses of American Crow populations to campgrounds in remote native forest landscapes. Journal of Wildlife Management. 68: 708-718.

Newton, I. 1998. Population limitation in birds. Academic Press, NY.

Nol, E. and **J. N. M. Smith.** 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. Journal of Animal Ecology 56: 301-313.

Overskaug, K., J. P. Bolstad, P. Sunde and **I. J. Oien**. Fledgling behavior and survival of Northern Tawny Owls. Condor 101: 169-174.

Perrins, C.M. and **R.H. McCleery.** 1985. The influence of age and pair bond on the breeding success of great tit *Parus major*. Ibis 127: 306-315.

Seddon, P. J. and **Y. M. van Heezik.** 1991. Hatching asynchrony and brood reduction in the Jackass Penguin: An experimental study. Animal Behaviour 42: 347-356

Slagsvold, T. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. Journal of Animal Ecology 53: 945-953.

Spear, L. and **N. Nur.** 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. Journal of Animal Ecology 63: 283-298.

Varland, D. E., E. K. Klass, and **T. M. Loughin**. 1993. Use of habitat and perches, causes of mortality and time until dispersal in post-fledging American Kestrels. Journal of Field Ornithology. 64: 169-178.

Van der Jeugd, H. P. and **K. Larsson.** 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledging characteristics. Journal of Animal Ecology 67: 953-966.

Verhulst, S. and **J. M. Tinbergen.** 1991. Experimental evidence for a causal relationship between timing and reproductive success of the great tit *Parvus m. major*. Journal of Animal Ecology 60: 269-282.

Webb, W. C., W. I. Boarman, and **J.T. Rotenberry.** 2004. Common Raven juvenile survivorship in a human augmented landscape. Condor 106: 517-528.

Williams, T. D., E. G. Cooch, R. L. Jefferies, and **F. Cooke.** 1993. Environmental degradation, food limitation and reproductive output. Journal of Animal Ecology 62: 766-777.

Wyllie, I. 1985. Post-fledging period and dispersal of young Sparrowhawks *Accipiter nisus*. Bird Study 32: 196-198.

Zammuto, R. M. and **J. S. Millar**, 1985. A consideration of bet-hedging in S*permophilus columbianus*. Journal of Mammology. 66: 652-660.

Table 3.1. Causes of death and longevity of life for post-fledging Common Ravens in Jackson Hole, Wyoming.

ID	Year	Julian Fledging Date	Days Alive Post-fledging	Cause of Death
11	2003	164	2	Head trauma
13[a]	2003	164	6	Unk. predation
14[a]	2003	160	1	Fox
18	2003	172	4	Coyote
26	2003	172	2	Coyote
37	2004	164	0	Head trauma
50	2004	169	4	Unk. predation
51	2004	170	3	Fox
54	2004	166	16	Human
56	2004	162	24	Broken wing

[a] Indicates birds from the same nest.

Table 3.2. Binary logistic regression results predicting survivorship of ravens during the post-fledging dependence period in Grand Teton National Park, Wyoming 2003-2004.

Predictor	Coefficient	St. Dev.	Odds Ratio	P-value
Constant	8.03	29.25		0.784
Fledge Date	-0.031	0.169	0.97	0.857
Nearest Neighbor Distance	-0.151	1.424	0.86	0.961
Nearest Road Distance	0.868	2.218	2.38	0.696
Nearest Subsidy Distance	-1.346	0.719	0.26	0.061
Body Condition Index	0.157	0.229	1.17	0.491
Brood Size				
2	-0.118	1.702	0.89	0.954
3	2.326	1.999	10.24	0.244
4	-0.879	1.625	0.42	0.589
5	0.182	1.864	1.2	0.922
Hatch Order				
2	0.054	1.017	1.06	0.958
3	0.518	1.457	1.68	0.722
4	-0.017	1.588	0.98	0.992
5	20	22984	3.23 E+8	0.999
Year	-0.067	0.976	0.94	0.945

Table 3.3. Binary logistic regression results predicting whether a nest was completely successful or partially successful in Grand Teton National Park, Wyoming 2003-2004.

Predictor	Coefficient	St. Dev.	Odds Ratio	P-value
Constant	-30.2	42.37		0.476
Fledge Date	0.2	0.249	1.22	0.422
Nearest Neighbor Distance	-0.165	1.55	0.85	0.916
Nearest Road Distance	-0.139	2.835	0.87	0.961
Nearest Subsidy Distance	-0.995	1.113	0.37	0.372
Brood Size				
2	-1.984	1.902	0.14	0.279
3	999	500011	-	0.998
4	-2.26	2.204	0.1	0.305
5	-0.299	1.890	0.74	0.874
Year	-0.159	0.1339	0.85	0.906

Table 3.4. Survival estimates of post-fledging juveniles to dispersal from natal territories in various bird species.

Species		Percent of Fledglings Surviving	*n*	Days Studied	Source
Ferruginous Hawks	*Buteo regalis*	89	18	40	Konrad and Gilmer 1986
Red Kite	*Milvus milvus*	87	37	40	Bustamante 1993
Common Raven	***Corvus corax***	**83**	**62**	**67**	**This Study**
American Kestrel	*Falco sparverius*	71	61	39	Varland et al. 1993
Prairie Falcon	*Falco mexicanus*	69	152	unknown	McFadzen and Marzluff 1996
Puerto Rican Parrot	*Amazona vittata*	67	15	209	Lindsay and Kalina 1994
Eastern Meadowlark	*Sturnella magna*	~63	50	90	Kershner et al. 2004
Greater and Coal Tits	*Parvus major* and *P. ater*	53	342	20	Naef-Daenzer et al. 2001
Black-billed Magpie	*Pica pica*	50	54	80	Husby and Slagsvold 1992
Northern Tawny Owl	*Strix aluco*	49	53	108	Overskaug et al. 1999
Common Raven	*Corvus corax*	38	240	~60	Webb et al. 2004
Yellow-Breasted Chat	*Icteria virens*	32	21	38	Alterman 2002
Common Blackbird	*Turdus merula*	~20	659	28	MacGrath 1991

Figure 3.1. Tarsus jesse transmitter attachment for fledgling Common Ravens using breakaway stitching to promote detachment after the transmitter battery expired. Jesse was attached to the tarsus using a zip-tie through the holes. Two holes in one side of the jesse accommodated potential variation in nestling and jesse size.

Figure 3.2. Kaplin-Meier survival estimates for juvenile Common Ravens (*n* = 62) for the first 66 days post-fledging for 2003 and 2004, combined. Male survivorship is shown with the dashed line and female survivorship is depicted with the solid line. Open circles indicate censored observations.

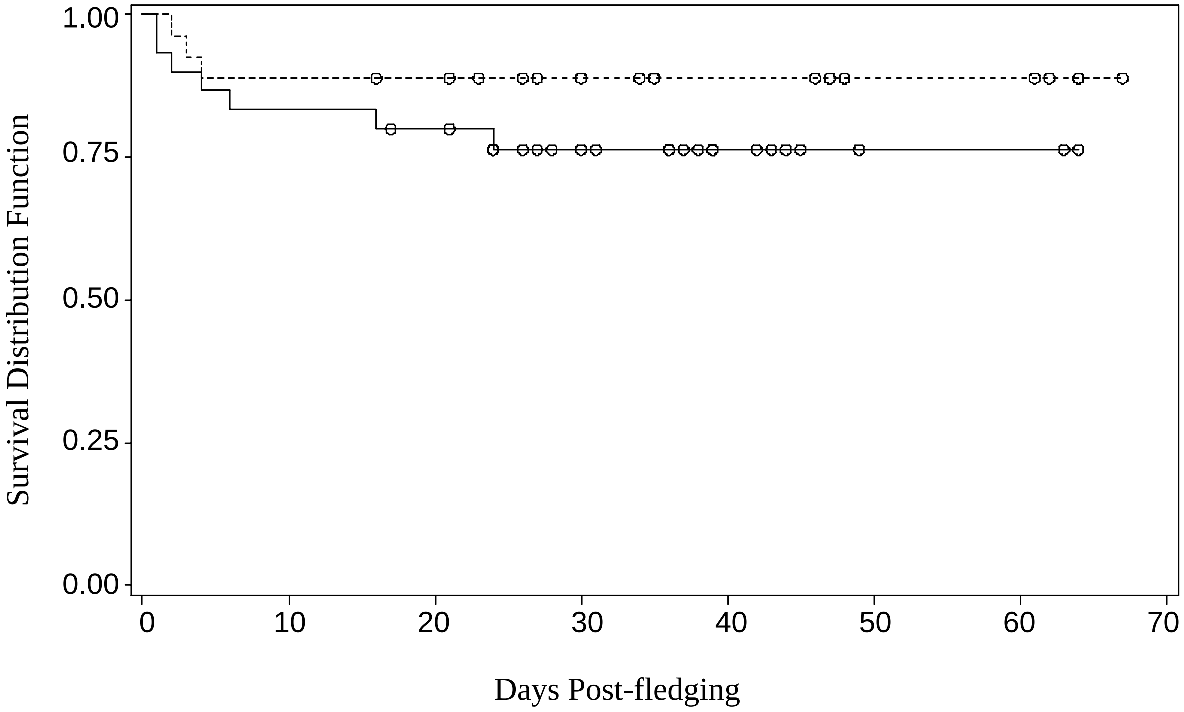


Figure 3.3. Box-plot of the distance of the nearest human settlement related to the nest and post-fledging survival of individual Common Ravens (*Corvus corax*) in Grand Teton National Park (2003-2004).

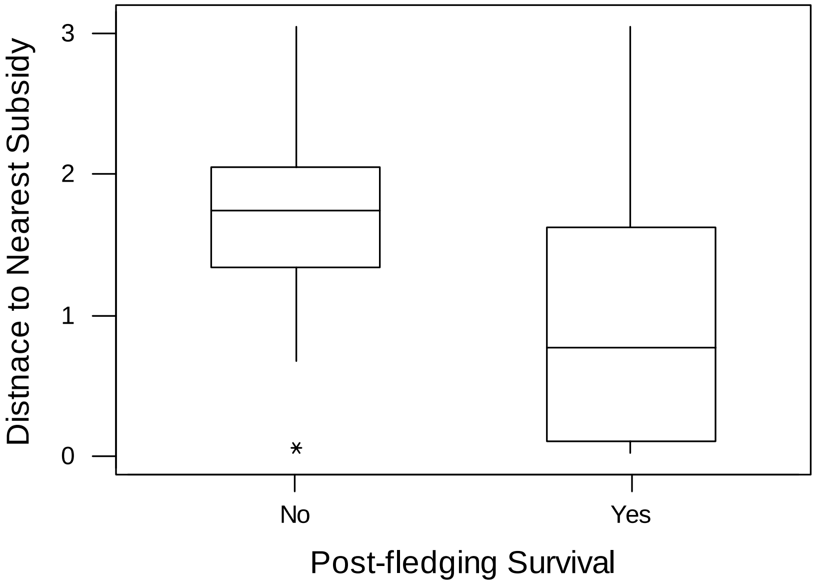


Figure 3.4. Box-plot of the fledging date related to post-fledging survival of individual Common Ravens (*Corvus corax*) in Grand Teton National Park (2003-2004).

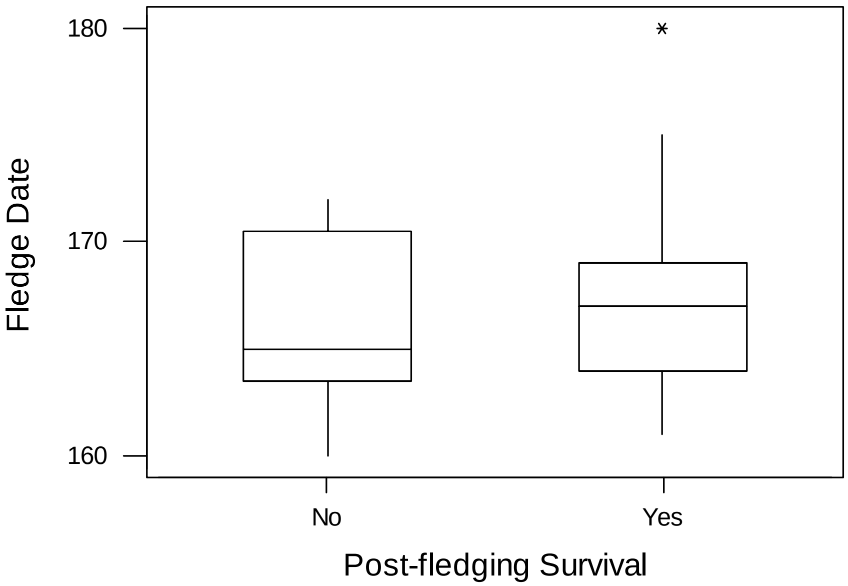


Figure 3.5. Box-plot of nestling body condition index related to post-fledging survival of individual Common Ravens (*Corvus corax*) in Grand Teton National Park (2003-2004).

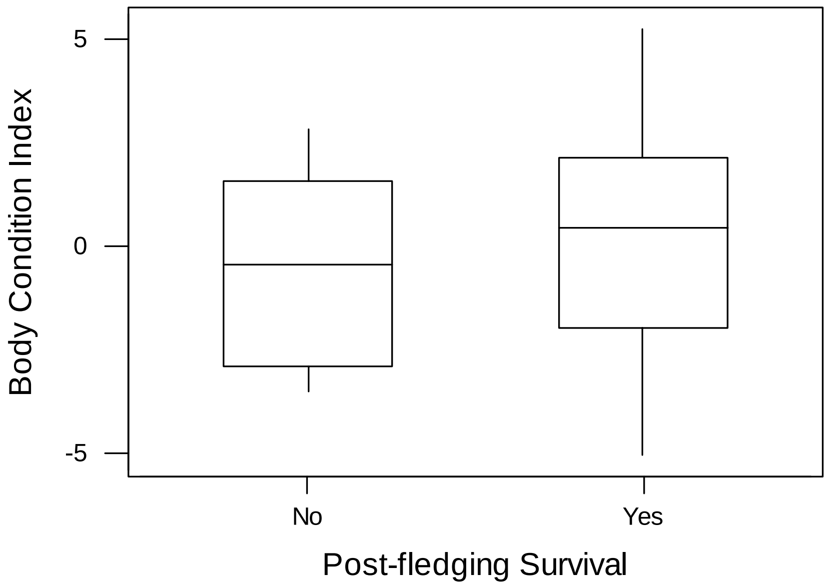


Figure 3.6. Box-plot of hatch order within a brood related to post-fledging survival of individual Common Ravens (*Corvus corax*) in Grand Teton National Park (2003-2004).

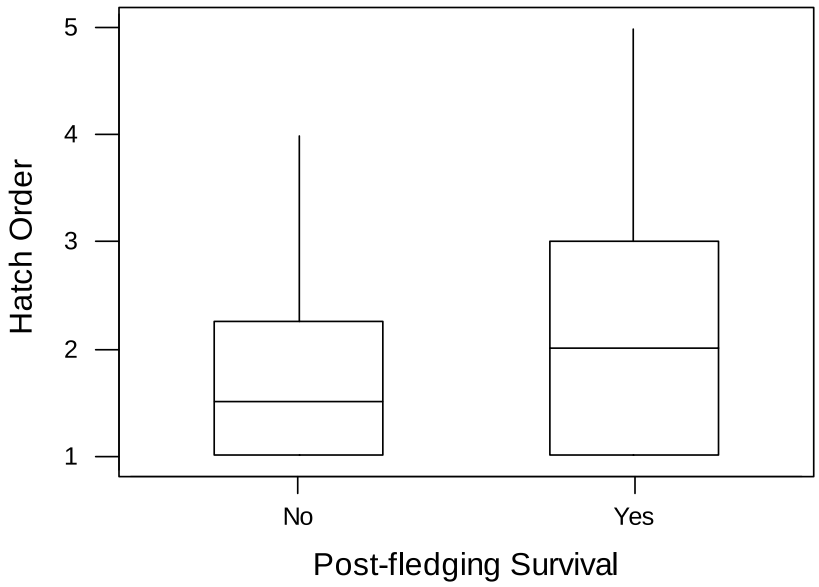


Figure 3.7. Box-plot of brood size related to post-fledging survival of individual Common Ravens (*Corvus corax*) in Grand Teton National Park (2003-2004).

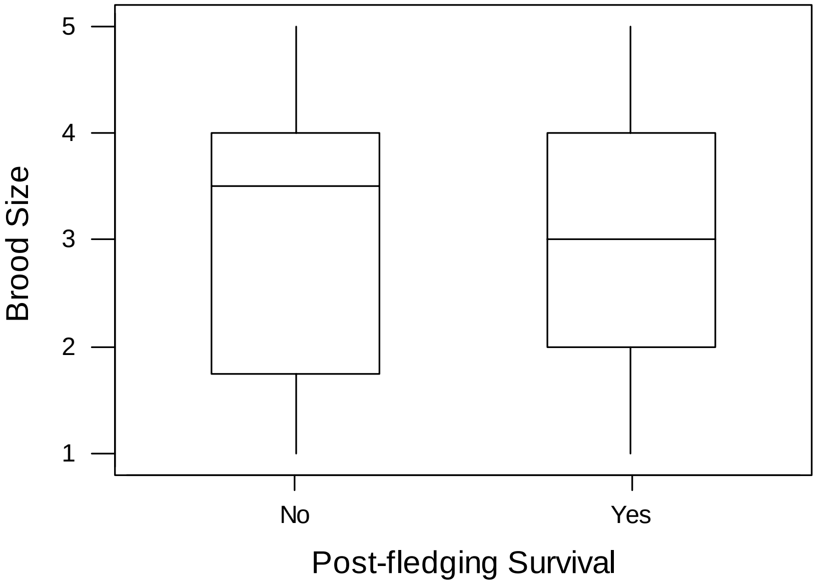


Figure 3.8. Box-plot of distance of a raven nest to the nearest nest of a conspecific related to post-fledging survival of individual Common Ravens (*Corvus corax*) in Grand Teton National Park (2003-2004).

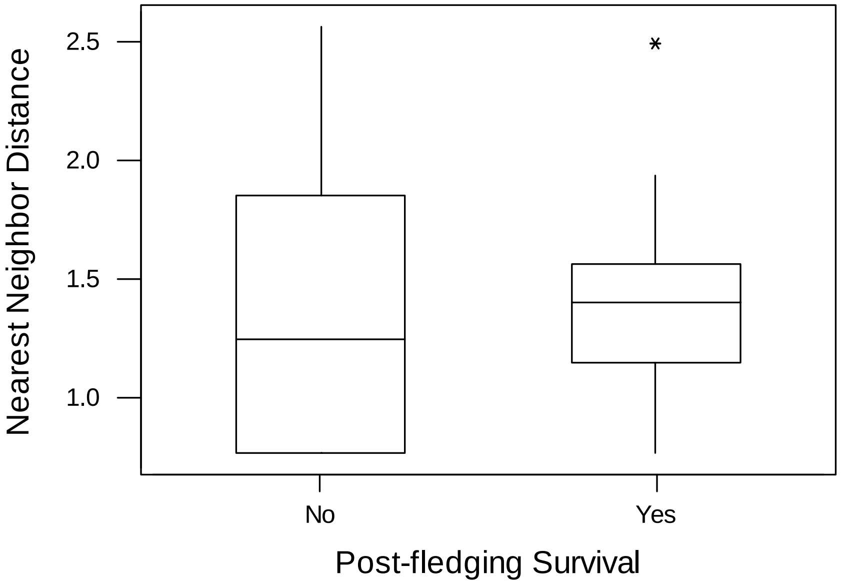
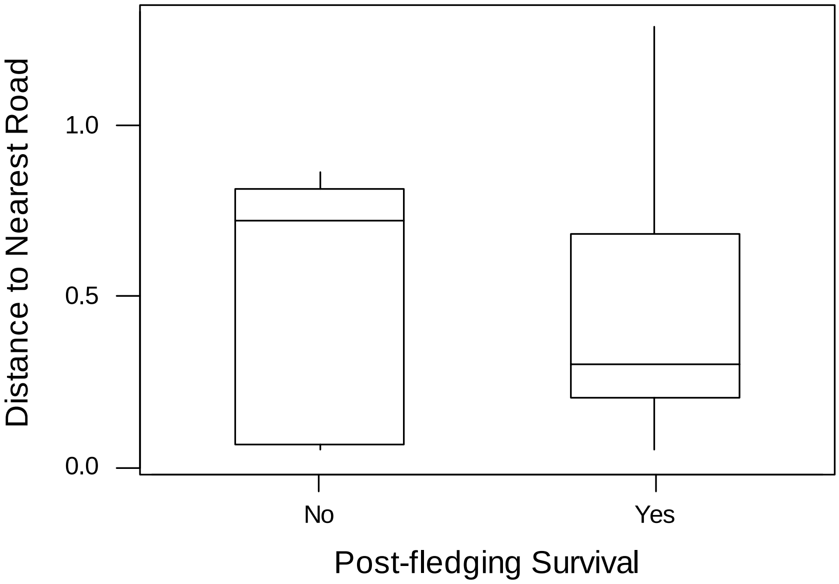


Figure 3.9. Box-plot of the distance of the nearest road to the nest related to post-fledging survival of individual Common Ravens (*Corvus corax*) in Grand Teton National Park (2003-2004).



Chapter 4

Post-fledging Movements, Sibling Associations, and Roosting Behavior of Common Ravens in Grand Teton National Park, Wyoming

Abstract

In 2003 and 2004, I studied a population of Common Ravens (*Corvus corax*) in Grand Teton National Park, Wyoming to examine the proximate causes for juvenile departure from their natal territories. I also monitored detailed movement patterns of the young ravens prior to departure and potential associations siblings had during the post-fledging dependence period. In 2004, I documented roosting behavior of the juveniles because of their tendency to return to their natal territories to roost after being absent from those territories during the day. I found that the onset of juvenile dispersal is likely influenced by food availability outside of natal territories, and possibly by brood size and gender, with larger broods and females dispersing earlier. I also found that 67% of fledglings studied (*n* = 34) came back to roost on their natal territories after making their first dispersal movement. Such behavior may prove beneficial for increased survivorship during the first few months after fledging due to decreased predation risks and social learning from communal roosting.

Introduction

The movements of juvenile birds during the post-fledging dependence period and the factors influencing these movements are poorly understood (Kenward et al. 1993).

Most studies have been dedicated to the dispersal timing, distance, and direction of juveniles after leaving the natal territory (e.g., Gonzalez et al. 1989; Morton et al. 1991; Caffrey 1992; Varland et al. 1993; Martinez and Lopez 1995; Minguez et al. 2001), few studies have investigated the movements of juveniles before dispersal from their natal territories (e.g., Kenward et al. 1993; Frumkin 1994; Kennedy and Ward 2002). Such movements can be important for understanding the strategies employed by each species to maximize the survivorship of the young. To understand the mechanisms behind increased survivorship of juveniles during the post-fledging period, I analyzed factors driving dispersal, juvenile movements, sibling associations, and roosting ecology of juvenile Common Ravens (*Corvus corax*) in that system.

Juvenile dispersal may be influenced by a variety of factors (Kenward et al. 1993). Proposed factors that may induce dispersal typically fall within two main categories: environmental and genetic influences (Howard 1960). Environmental factors may include seasonal weather changes (Berthold 1993), food shortages (Nilsson and Smith 1985; Part 1990; Kenward et al. 1993), or aggression towards the disperser from either the parents or siblings (Kenward et al. 1993). Alternatively, and likely not exclusively, young birds may be genetically predisposed to disperse at a specific age (Howard 1960).

If a species is dependant on some seasonality change, such as photoperiod changes, then it would be reasonable to predict that there would be little variation in dispersal dates of individuals within a year. If food supply is the main factor driving dispersal, two optional patterns may be expressed. First, individuals that are experiencing limited resources may leave their territory earlier relatively early to avoid starvation (Part

1990). Conversely, a juvenile may opt to stay in its natal territory to forage until it has developed full flight capabilities, leading to a longer dependence period during years of low food availability (Table 4.1; Nilsson and Smith 1985).

Patterns of fledgling dispersal initiated because of aggression may differ depending on who is the aggressor. If a parent is the aggressor, then all of the fledglings should leave the natal territory at about the same time, but departure dates of between nests should vary. This possible motivation to disperse can be differentiated from the hypothesis that dispersal is caused by a food shortage with multiple year data. If parental aggression is driving dispersal, then that territory should have dispersal dates similar across years. Whereas, dispersal consistently caused by food shortages would not necessarily produce consistent dispersal dates among years. If a sibling was the aggressor, then each nest with more than one fledgling should have large variation in dispersal times among broodmates, with the variation increasing with more nestlings. Also, nests with one fledgling should disperse later than the first disperser in multiple fledgling broods.

Juvenile dispersal may also be driven by predisposed, innate factors, either entirely or in part (Howard 1960). If this is the case, then it would be reasonable to assume that offspring from the same parents would disperse at about the same time after fledging, regardless of year. Dispersal explained by those ideas should mirror predictions from the parental aggressor hypothesis, but have low variability in departure, as it relates to brood size (Table 4.1).

Increased juvenile survivorship may not only be a factor favoring various dispersal reasons, but also a function of family group associations during the dependence period. Possibly, juveniles may experience lower predation risks by having close associations with siblings, and therefore, increased vigilance in a group. Also, because ravens are such a social species (Ratcliffe 1997), juveniles may learn valuable lessons about social interactions during the post-fledging period which may increase long term survivorship. Another factor that may positively influence survival of the young is the roosting behavior of a family group because of benefits related to predation deturance and future social interactions. A juvenile may procure a relatively safe roosting location with its family group rather than the least preferred and lass safe roosts at the communal roosts, where most juveniles sleep (Buckley 1998).

In this study, I have investigated juvenile departure of the Common Raven (*Corvus corax*) from their natal territories in Jackson Hole, Wyoming. Also, I have mapped detailed movements of the young during the fledging-dependence period to attain information on how juveniles gain flight and food acquisition skills. I also report results of roosting locations of the young during this period to better understand the ecology of the fledging-dependence period. Lastly, I report information on association behavior of fledglings during this time period, both within broods and among broods.

Methods

Study Area

The study area encompasses approximately 181 km^2 of a mountain valley in the southwest corner of Grand Teton National Park (GTNP), which is situated in northwest Wyoming (43º91’N, 110º40’ W). Elevations of the mountain valley range from 1932 to 2343 m, with the Teton Range to the west and Gros Ventre Range to the east. To the north lies the Yellowstone National Park plateau and the town of Jackson, Wyoming (population ca. 8700) is located 8.8 km to the south of the point where the two mountain ranges converge. The study area contains the Snake River corridor and an isolated, forested butte. See Chapter 3 for further details.

Banding and Tracking

In order to follow the young ravens after fledging, I placed leg-mount transmitters (Holohil Ltd., Carp, Ontario) on nesting ravens one week prior to estimated fledging using a leather jesse (6.0 g finished mass). The jesse was cut in half and re-stitched together with cotton thread, coated in wax, to provide a breakaway system for the transmitter (Chapter 3; Figure 3.1). I individually color coded the antennas with shrink tubing (3M, St. Paul, MN) for ease of identification.

If a nestling died before fledging, or if a fledgling died shortly after leaving the nest, the transmitter was removed, cleaned, and placed on another nestling from a different nest that had not yet fledged to maximize sample size. All of the young from 27 accessible nests were fitted with transmitters in 2003 and 2004.

After the young were banded, nests were monitored at least once every 2 days to determine fledging date and to make certain that the young had not died prior to fledging. I attempted to obtain visual confirmation of nestlings for all banded young during this period. After the first nestling had fledged from a nest, I monitored that nest every day until I determined that all of the nestlings had fledged and could fly from perch to perch. From that point until shortly before the onset of natal dispersal, I obtained visual confirmation on each fledgling's location every 2-3 days. When young demonstrated extended flights (>1.5 km) and seemingly were capable of departure, I documented locations daily. Any fledgling flying more than 3 km away from the nest site without returning for three consecutive days or nights was classified as successfully departed (modified definition from Wyllie 1985). If a fledgling was observed to move more than 3 km from its nest site during the day, subsequent roost locations were obtained to confirm juvenile departure. All locations were transferred into ArcView GIS (Environmental Systems Research Institute Inc., Redlands, CA), from which distances from the nest were measured and departure patterns were mapped.

Upon visual contact with the fledglings, I recorded their behavior (i.e., perched, flying, walking, allopreening, foraging), associations with siblings and parents, and described flight capabilities (if seen). Siblings were recorded as by themselves if no siblings were within 40 m. While two siblings that close may be in vocal or visual contact, I considered this distance to represent a minimum distance, and therefore a conservative measure of associations. By an individual being 40 m or greater from its sibling(s), it is possible that it may want to associate with the group, but is being excluded from having close ties to its siblings. I limited the time spent in the vicinity of the birds to 10 minutes to minimize disturbance. Roosting “locations” were an indicator of the presence or absence of the fledgling within 3 km of its nest site, not triangulated locations.

In 2003, I observed that fledglings would return to roost in their natal territory after spending all day in areas beyond telemetry range. Because this was observed late in the post-fledging period of 2003, data on roosting locations in natal territories for 2003 is less complete than the roosting data for 2004. Importantly, the determination of a departure event is influenced by whether data on roosting locations for the fledglings are considered or not. In previous fledgling dependence departure studies (e.g., Kenward et al. 1993; McFadzen and Marzluff 1993; Kershner et al. 2004; Webb et al. 2004), fledgling locations were not monitored after dusk, so fledglings returning to roost at their natal site were probably overlooked. In 2004, I attempted to obtain roosting locations for each fledgling at least every other day, including after fledglings departed from their natal areas during the day, so a complete data set exists for 2004. Thus, I analyzed the 2003 and 2004 data combined for time to the first departure event, which I define as the first diurnal movement over 3 km away from the nest. While this may not reflect the true departure date of the fledglings because of subsequent returns for roosting, it reflects the cessation of direct parental care and represents an index for the length of the post-fledging dependence period. I used *t*-tests to test for associations between family group size and first departure movements and a Mann-Whitney *U* to test the variability of first dispersal movements between years. I tested the potential affect of juvenile gender on the time until first departure movements and whether a gender affects the tendency to roost at its natal site after the first departure event with binary logistic regression. I used paired *t*-tests to determine if a territory that produced fledglings in both 2003 and 2004 had similar first departure dates. I assumed for these tests that the breeding adults of these territories likely involved the same individuals between years (Chapter 3; Ratcliffe 1997).

Results

Pre-departure movements and sibling associations

I tracked 59 juvenile ravens from 27 nests during their post-fledging dependence periods in 2003 and 2004. Typically, fledglings could not fly well enough to escape mammalian predators when they left the nest for approximately 2 days (range = 0-5 days). On three occasions, fledglings flew so poorly that they were captured and killed by mammalian predators (0-5 d; Chapter 3). Including the birds with unknown fates (death and loss or failure of transmitter), all birds stayed within 720 m of the nest for at least 15 days post-fledging (Figure 4.1).

In 2003, I obtained 307 visual locations on 28 fledglings from 10 nests. Of those 28 fledglings, I found five dead. In addition, one transmitter failed prior to juvenile departure. I recorded 275 individual locations in which the juvenile monitored had a live sibling. Of those 275 locations, only 3.3% involved a juvenile that was not in the immediate vicinity of all of its surviving nest mates. Of those nine locations in which the family groups were not closely associated, four had partial associations (two groups of siblings at least 40 m apart) among brood mates and five were of a juvenile by itself. There were no instances were siblings were greater than 100 m apart before the first dispersal movement from any family group monitored. All siblings left their nest on the same day except for one nest in which one nestling left 3 days ahead of its sibling.

I obtained 536 locations from 32 fledglings (14 nests) in 2004. That year, there were 425 locations when I located a juvenile that had at least one sibling alive at the time. Of those locations, 21 (4.9%) were locations of siblings that were not within 40 m of all of its siblings. As with 2003, I found no instances of siblings being greater than 100 m apart before departure. One family group with five fledglings comprised almost half of these locations (10 of 21), and four locations of the ten were of fledglings near one other sibling, but away from the other three. There was more variability of fledging in 2004, with only half of the eight nests that had at least two fledglings that departed the nest on the same date. Siblings in the other four nests fledged from 1-6 days apart.

Departure Events

Of the 28 fledglings that I tracked in 2003, natal territory departures were documented for 23 fledglings from 10 nests. In 2004, I was able to track 22 fledglings from nine nests to departure. All fledglings that were not monitored to departure were either found dead prior to initial dispersal (n = 10) or their transmitters failed (n = 3). The first movement of a fledgling greater than 3 km from the nest was 19 days post-fledging in 2003 and 18 days in 2004.

In 2003, the mean time until the first departure movement (FDM) was 27.2 days after fledging (range = 19-36 days). Six of seven family groups had FDMs on the same day. One family with two fledglings had a difference of 3 days in the FDMs, between the two juveniles. A family group with five fledglings exhibited relatively delayed FDM (38 days) compared to the other family groups. The other three broods monitored in 2003 had only one surviving fledgling.

The mean FDM in 2004 was 41.1 days post-fledging, with a range from 19-54 days. I found no difference in FDMs among group sizes for 2004 at the 95% confidence using a Mann-Whitney U test. The variability within family groups was greater in 2004, with the mean variability of 4.1 days (range = 0-12 d).

I found that the mean time to FDM occurred earlier in 2003 than in 2004 (t = 5.61, df = 44, P < 0.001). Likewise, the degree of variability was less in 2003 than in 2004 (S.D. = 4.68 and 9.77 in 2003 and 2004, respectively; P = 0.002; Figure 4.2).

Between 2003 and 2004, the variability of FDM within nests approached significant differences, with 2003 showing less variability (t = 2.03, df = 12, P = 0.066). In 2003, there was no relationship between gender and FDM (mean = 25.4 days for females and 28.9 for males; P = 0.108), but in 2004, FDM was approaching significance in predicting gender, with the females leaving earlier (mean = 36.9 days for females vs. 46.2 days for males, P = 0.080, z = 1.75). I monitored three nests that produced dispersers successfully in both 2003 and 2004. For these three nests, the FDM dates were earlier in 2003 (mean = 25.5 days) than in 2004 (mean = 33.0 days). For all nests, I found no relationships between fledging and dispersal dates when years were combined (Figure 4.2, P > 0.05). However, the mean FDM had a weak, positive relationship to brood size for both years, combined (Figure 4.3, P = 0.039, r^2_{adj} = 0.18). I also found that FMD was related to brood size, fledging date, and gender in a multivariate manner (P = 0.039, r^2_{adj} = 0.12).

Roosting ecology of the fledglings during the post-fledging dependence period

In 2003, I observed that while fledglings were not located within 3 km of their nest sites during the day, some returned to roost with their parents within their natal territory. In 2004, I located all roosting nestlings after the FDM was made by fledglings. That year, the tendency for a juvenile to return to roost at the natal site was family group specific. In six of nine family groups, all of the fledglings returned to roost after the FDM for at least one night (mean = 9.2 nights post-FDM; range = 1-21 nights; n = 13 fledglings). No fledglings in the other three nests ever came back to roost after their FDM.

Post-fledging Brood Parasitism

On one occasion in 2003, I observed two incidents of "post-fledging brood-parasitism" (Frumkin 1994). A brood of four fledglings (the *west* family group) from an early nesting pair split up into two groups of two juveniles each at 29 days post-fledging. Group *West A* consisted of the breeding adults and two young that stayed near the natal territory and group *West B* consisted of the other two fledglings. Group *west B* was sighted 4.8 km from their nest, but with another family group (*Barn*) that consisted of three fledglings and the adults. Both groups *West B* and *Barn* were observed feeding at an elk (*Cervus canadensis*) carcass. The *Barn* fledglings and group *West B* were all begging from the *Barn* adults that were feeding on the carcass. Although I observed no direct feedings of the *West B* juveniles that day, I located these two individuals roosting in the barn where the *Barn* birds had nested that year, and with that family group.

The following day, I located all five juveniles at the carcass again with the *Barn* adults. The adults fed their own young, as well as provided at least three feedings to each of the *West B* juveniles. That night, the group B was not located either at the *Barn* or the *West* natal territory. Five days later, I found one of the *West B* juveniles from roosting back at its natal site for the last time. Ten days after the *West B* group was roosting with the *Barn* birds, the second bird from the *West B* group tried again to roost with the *Barn* ravens, but was denied access to the roosting barn through aggressive chases by the *Barn* adults. I did not observe any other attempts by this juvenile to roost with the *Barn* family group.

Discussion

During the first two weeks after fledging, young ravens stay within a 720 m radius of their nest sites. Most likely, this corresponds with the natal territory size of fledgling ravens (Kristin 2001; Webb et al. 2004). This pattern of staying close to the natal territory for the first two weeks is evident in many taxa of birds (e.g., Beske 1982; Morton et al. 1991; Husby and Slagsvold 1992; Frumkin 1994). Kenward et al. (1993) suggested that juveniles may not move beyond the natal territory until the completion of flight feather growth, which could explain why no ravens left prior to two weeks post-fledging. However, after this 2 week period of residence, there appears to be no pattern of departure timing based on fledging date (Figure 4.2) or gender. I did find an inverse relationship between departure date and brood size (Figure 4.3), indicating that feather growth completion may not be the sole factor related to departure.

The variation in juvenile dispersal patterns were consistent with the hypotheses of both the food resource and environmental stimulated dispersal (Table 4.1). Because there was a great deal of variability between nests each year, dispersal timing based on large-scale weather events or a need for escape from adverse weather were not likely. This was also supported by the fact that ravens did over-winter in this region (B. Bedrosian, unpubl. data). Nonbreeding ravens typically exhibit nomadic movements to follow food supplies (Heinrich 1994), so it is feasible that juvenile ravens on poor-quality territories dispersed earlier to find other food resources. Unfortunately, I have no quantitative data on food resources within individual territories to test this hypothesis.

Collectively, all raven territories may experience poor food resources when compared to other localized areas, where there is an overabundance of food due to the large foraging areas of ravens. This is the pattern I observed from 2003, when there were outbreaks of both army cutworm moths (*Euxoa auxiliaris*) at high elevations throughout the Rocky Mountains (Coop et al. 2005) and Mormon crickets (*Anabrus simplex*) at low elevations. The cutworm moth migration occurred at elevations greater than roughly 3000 m in the Teton Range (R. Jackson, Grand Teton National Park Lead Climbing Ranger, Pers comm.), which runs parallel to the western study area border, beginning in May. Common Ravens have been noted to key in on migrations of cutworms, and have remained in the alpine areas as long as 2 weeks after the migration has passed (Hendricks 1998). In 2003, the majority (74%) of the first dispersal movements of juveniles were into higher elevations of the Tetons. This was not the case for the juveniles of 2004, I received reports from back-country users that the moths were not nearly as numerous that year (R. Jackson, pers. comm.).

In Jackson Hole, 2003 was also the third consecutive invasion year for Mormon crickets. Infestations occurred in two particular areas outside of most nesting areas and were large enough to make headlines in local papers ("Hoppers eating their way across National Elk Refuge;" Jackson Hole News and Guide; 3 July 2003). However, I did not witness the largest infestations until late July. Beginning on 30 July, I regularly observed groups of ravens (including banded juveniles) with 8-26 individuals feeding on road-killed crickets in the mornings within the study area. Due to greater amounts of rainfall during the summer of 2004, there were no outbreaks of Mormon crickets in 2004. Likewise, I did not observe any large groups of ravens in the study area prior to September. While evidence strongly suggests that food was a primary factor driving dispersal in 2003, it appears that juvenile departure was influenced more by other environmental factors such as weather patterns than food resources in 2004 (Table 4.1).

Circumstantial evidence supports the supposition that juvenile ravens may have dispersed earlier in 2003 in response to food availability. Similar patterns have been documented in Northern Goshawks (*Accipiter striatus*), where juveniles left earlier when food was lacking in their natal territories (Kenward et al. 1993). However, I suggest that food may not have been lacking in natal territories, but an overabundance of food may have existed outside of natal territories for ravens in Wyoming. In both food driven scenarios, food resources are more abundant outside of the natal territory, so early juvenile departure would be advantageous for increased survivorship based on obtaining easier food resources. Breeding adults may have been keyed into these resources outside of their nesting territory by seeing other ravens flying over to the areas of abundant food.

Similar to Red Kites (*Milvus milvus*; Bustamante 1993), juvenile ravens often return to their natal territories to roost after their initial departure. Without documentation of roosting locations for juveniles during and after the fledging period, the time until complete independence may be underestimated. I do not know if this pattern was more prevalent in 2003, when the FDMs were earlier. The latest FMD in 2003 was 35 days, while only one nest in 2004 had FDMs less than 35 days. The fledglings from this early nest in 2004 all returned to roost at their natal site after the FDM for 8-19 nights after the FDM. Because the juveniles were leaving the natal area earlier in 2003, it is possible that they were more likely to return to roost with their parents because their food acquisition skills and social skills are not as developed as fledglings that stay longer on their natal territories. Further documentation is needed to evaluate patterns between FDM and the tendency for roosting only at the natal site after the FDM.

My data suggested that there may be a variety of benefits for juveniles to use roosting locations within a natal territory, even after the FDM. First, by returning to roost with its parents, a juvenile may learn of new food resource locations through information sharing (Marzluff et al. 1996). Second, juveniles may take advantage of the relative safety from predation by returning to a known roosting location with other birds (their parents; Donnazar and Feijoo 2002). While roosts of sub-adult and non-breeding ravens exist during the summer (Boarman and Heinrich 1999) and may offer some similar benefits, the advantages gained from roosting with kin may outweigh the benefits of roosting with non-related individuals. In communal roosts, birds naïve of a food resource have to pursue knowledgeable ravens to a resource (Heinrich 1994), while parents still providing parental care may actively lead their young to a resource. Also, there is intraspecific competition for preferred roosting sites within a communal roost of non-related individuals (Buckley 1998), and young of the year would most likely occupy inferior locations. Given the alternative of roosting by itself in a relatively unknown area, communally roosting with non-related individuals, or returning to roost in a familiar territory with family members, the most beneficial scenario would likely be the latter.

By engaging in communal roosting behavior with kin, I suspect that juvenile ravens begin to learn the benefits of roosting with conspecifics. However, communal roosting with kin may occur for reasons different than communal roosting with non-kin. I suggest that juveniles roost with their parents for benefits outlined by the “two-strategies hypothesis” (Weatherhead 1983), in which the juveniles receive food information transfer and a predation buffer. Communal roosts of non-related ravens occur as an information transfer (Ward and Zahavi 1973; Marzluff et al. 1996; Marzluff and Heinrich 2001), and the following of knowledgeable individuals by naïve individuals (Marzluff et al. 1996) may be learned early by juveniles following their parents.

Because of the gregarious nature of food acquisition in ravens (Ratcliffe 1997; Boarman and Heinrich 1999) and their generalist diet (Boarman and Heinrich 1999), there seems to be little need for maturation of specific food acquisition skills (e.g., specialized hunting skills) in juveniles. Such specialization may lead to specific dispersal timing based on the time needed to acquire adequate hunting skills for a particular food item (Bustamante 1993). More likely, completion of flight feather growth may be indicative of when the juveniles are capable of adequate flight abilities and departure if the food conditions are right. My data supported the hypothesis that food resources, both inside and outside the natal territory, may be the primary factor driving juvenile departure during the post-fledging period. Further, my data support the hypothesis that dispersal is initiated earlier by females, which may lead to gender biased natal dispersal.

Literature Cited

Beske, A. E. 1982. Local and migratory movements of radio-tagged juvenile harriers. Raptor Research 16: 39-53.

Berthold, P. 1993. Bird Migration: A General Survey. Oxford University Press, NYC.

Boarman, W. I. and **B. Heinrich.** 1999. Common Raven (*Corvus corax*) *in* The Birds of North America, No 476 (A. Poole and F. Gill, eds.) The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Buckley, N. J. 1998. Interspecific competition between vultures for preferred roost positions. Wilson Bulletin 110: 122-125.

Bustamante, J. 1993. Post-fledging dependence period and development of flight and hunting behavior in the Red Kite (*Milvus milvus*). Bird Study 40: 181-188.

Caffrey, C. 1992. Female-biased delayed dispersal and helping in American Crows. Auk 109: 609-619.

Coop. J. D., C. D. Hibner, A. J. Miller, and **G. H. Clark.** 2005. Black bears forage on army cutworm moth aggregations in the Jemez Mountains, New Mexico. Southwestern Naturalist 50: 278-281.

Donnazar, J. A. and **J. E. Feijoo.** 2002. Social structure of Andean Condor roosts: influence of sex, age, and season. Condor 104: 832-837.

Fridolfsson, A-K and **H. Ellgren.** 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Bioogy 30: 116-121.

Frumkin, R. 1994. Intraspecific brood-parasitism and dispersal in fledgling Sparrowhawks *Accipiter nisus*. Ibis 136: 426-433.

Gonzalez, L. M., B. Heredia, J. L. Gonzalez, and **J. C. Alonso.** 1989. Juvenile dispersal of Spanish Imperial Eagles. Journal of Field Ornithology 60: 369-379.

Heinrich, B. 1994. Does the early Common Raven get (and show) the meat? Auk 111: 764-769.

Hendricks, P. 1998. A migration of Adult Army Cutworms, *Euxoa Auxiliaris* (Grote) (Lepidoptera: Noctuildae) at High Elevation. Canadian Field-Naturalist 112: 165-166.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist 63: 152-161.

Husby, M. and **T. Slagsvold.** 1992. Post-fledging behaviour and survival in male and female Magpies *Pica pica*. Ornis Scandinavica 23: 483-490.

Kennedy, P. L. and **J. M. Ward.** 2002. Effects of experimental food supplementation on movements of juvenile northern goshawks (Accipiter gentiles atricapillus). Oecologia 134: 284-291.

Kenward, R. E., V. Marcstrom, and **M. Karlbom.** 1993. Post-nesting behavior in goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest switching. Animal Behaviour. 46: 371-378.

Kershner, E. L., J. W. Walk, and **R. E. Warner.** 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*). Auk. 121: 1146-1154.

Martinez, J. A. and **G. Lopez.** 1995. Dispersal and causes of mortality of the Barn Owl (*Tyto alba*) in Spain. Ardeola 42: 29-37.

Marzluff, J. M. and **B. Heinrich.** 2001. Raven roosts are still information centres. Animal Behaviour 61: F14-F15.

Marzluff, J. M., B. Heinrich, and **C. S. Marzluff.** 1996. Raven roosts are mobile information centres. Animal Behaviour 51: 89-103.

Mcfadzen, M. E. and **J. M. Marzluff.** 1996. Mortality of Prairie Faclson during the fledging-dependence period. Condor 98:791-800.

Miguez, E., A. Angulo, and **V. Siebering.** 2001. Factors influencing the length of the post-fledging period and timing of dispersal in Bonelli's Eagle (*Hieraaetus fasciatus*) in southwestern Spain. Journal of Raptor Research 35: 228-234.

Morton, M. L., M. W. Wakamatsu, M. E. Pereyra, and **G. A. Morton.** 1991. Postfledgling dispersal, habitiat imprinting, and philopatry in a montane, migratory sparrow. Ornis Scandinavica 22: 98-106.

Nilsson, J. X. and **H. G. Smith.** 1985. Early fledgling mortality and the timing of juvenile dispersal in the Marsh Tit *Parus palustris*. Ornis Scandinavica 16: 293-298.

Part, T. 1990. Natal dispersal in the Collared Flycatcher: Possible causes and reproductive consequences. Ornis Scandinavica 21: 83-88.

Ratcliffe, D. 1997. The raven. Academic Press, San Diego.

Varland, D. E., E. E. Klaas, and **T. M. Loughin.** 1993. Use of habitat and perches, causes of mortality and time until dispersal in post-fledging American Kestrels. Journal of Field Ornithology 64: 169-178.

Ward, P. and **A. Zahavi.** 1973. The importance of certain assemblages of birds as 'information centers' for food-finding. Ibis 115: 517-534.

Weatherhead, P. 1983. Two principle strategies in avian communal roosts. American Naturalist 121: 237-243.

Webb, W. C., W. I. Boarman, and **J.T. Rotenberry.** 2004. Common Raven juvenile survivorship in a human augmented landscape. Condor 106: 517-528.

Wyllie, I. 1985. Post-fledging period and dispersal of young Sparrowhawks *Accipiter nisus*. Bird Study 32: 196-198.

Zammuto, R. M. and **J. S. Millar.** 1985. A consideration of bet-hedging in *Spermophilus columbianus*. Journal of Mammology. 66: 652-660.

Table 4.1. Predictions about variability of first departure movements from various hypotheses on mechanisms of juvenile dispersal, and observed patterns of variability in a population of Common Ravens (*Corvus corax*) in Jackson Hole, WY 2003-2004.

	Causes for juvenile dispersal					
Variability	Food outside natal site	Other environmental conditions[a]	Parental aggressor	Sibling aggressor	Innate behavior	Observed patterns
Within Nests	Low	Low	Low	High	Low	Low
Among Nests	Low	High	High	Variable	High	Variable[b]
Among Years	High	High	Low	Low	Low	High
Within Nests; Across Years	High	High	Low	Low[c]	Low	High
In Relation to Brood Size	Low	Low	High	High	Low	Low

[a] Seasonal changes.

[b] Low variability in 2003 and high variability in 2004.

[c] Assumes equal brood size among years.

Figure 4.1. Distances of radio-tagged fledgling Common Ravens from their nests during the post-fledging period in 2003 and 2004. Juveniles > 3 km from their nest represent juvenile departure from their natal sites.

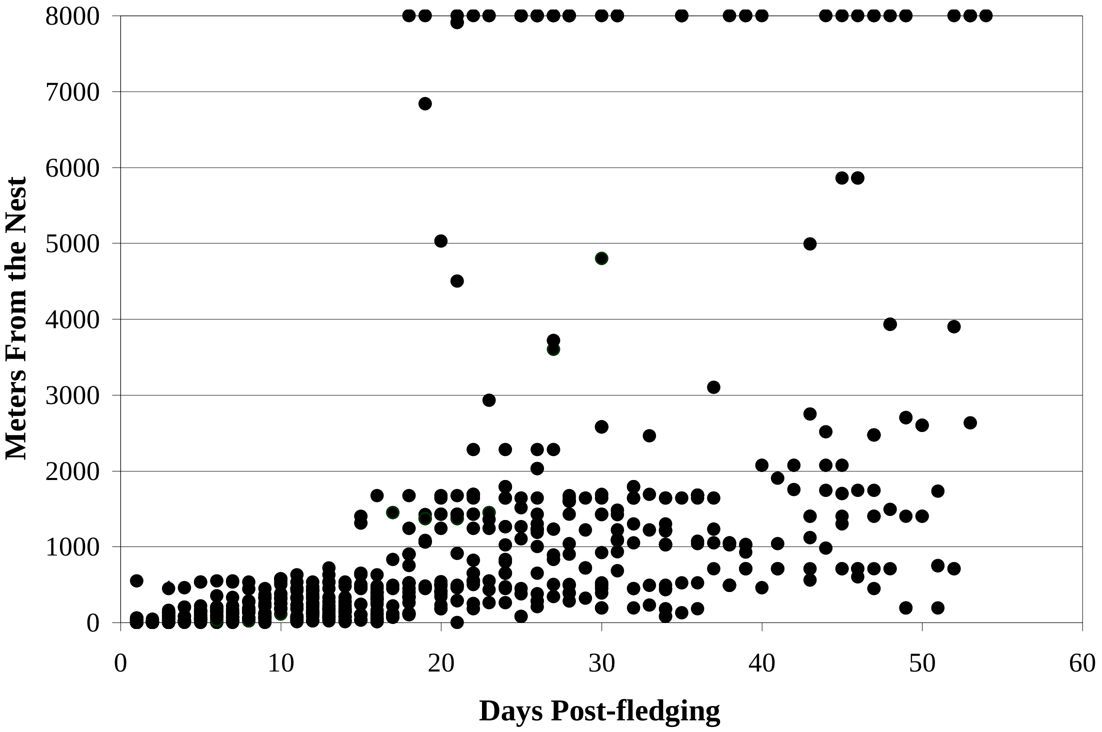


Figure 4.2. Mean date of departure from natal area plotted against mean fledging date of juvenile Common Ravens in Grand Teton National Park, Wyoming in 2003-2004.

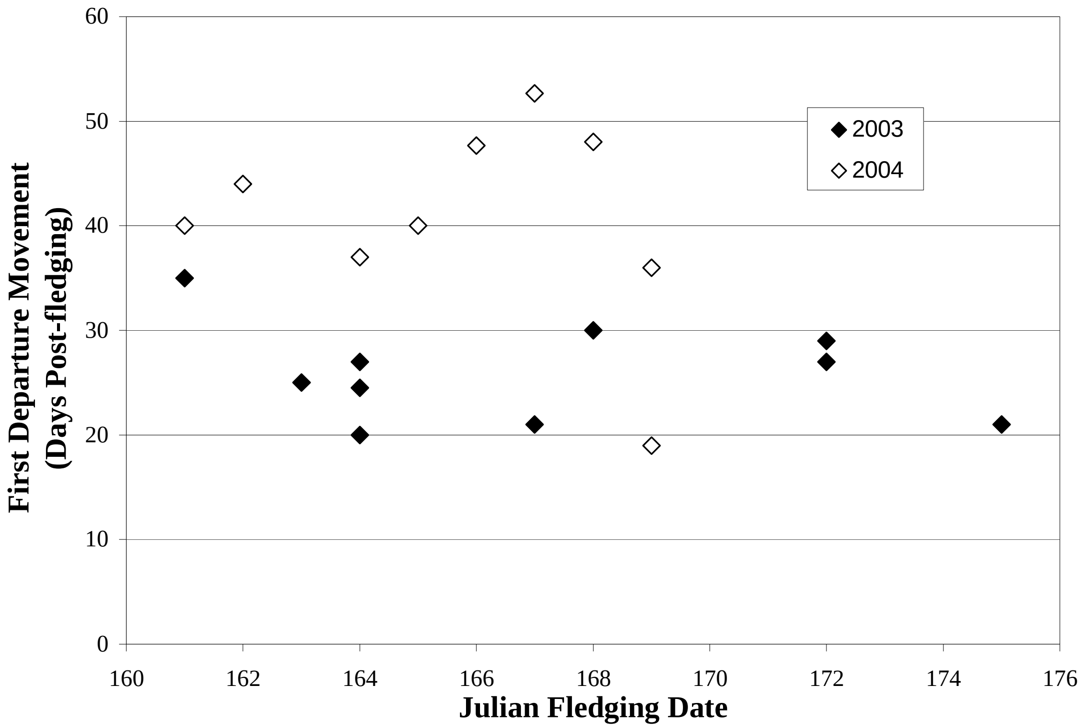
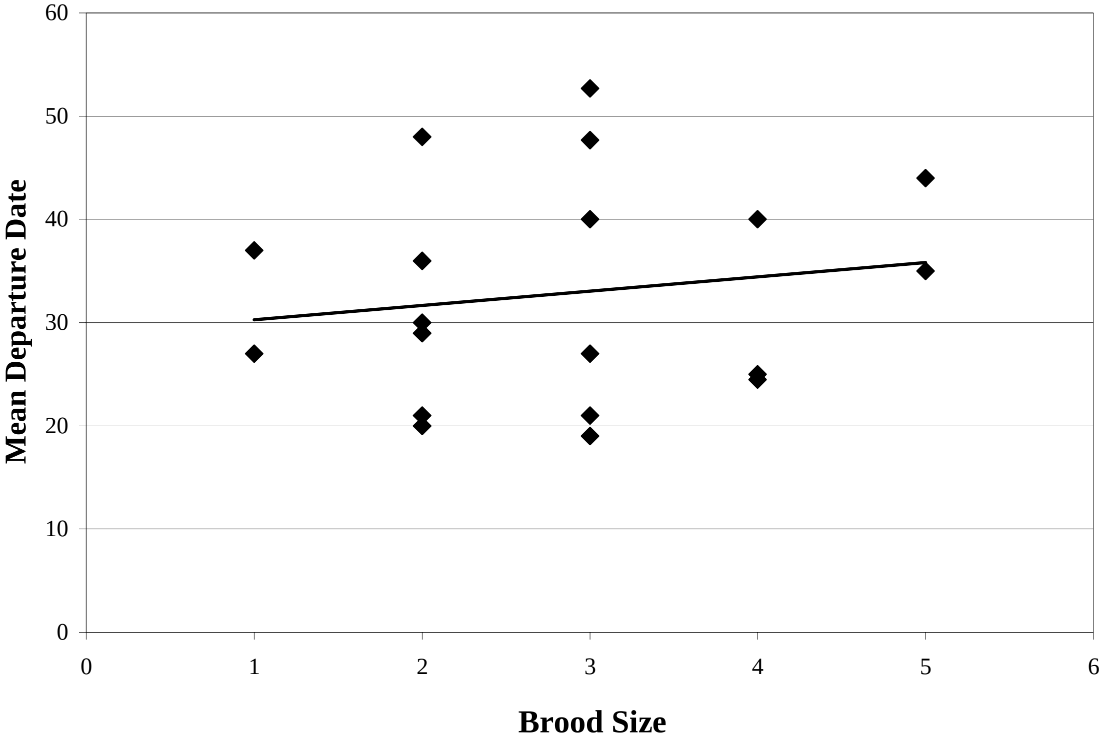


Figure 4.3. Mean nest departure dates plotted against brood size for Common Raven fledglings in Grand Teton National Park, Wyoming for 2003-2004. Regression line indicates slight, positive trend (P < 0.05).



Chapter 5

General Conclusions

Historically, Common Ravens (*Corvus corax*) have been obligate predators, relying heavily on large mammals for food resources during the winter months in northern latitudes (Boarman and Hienrich 1999, Stahler et al. 2002). The historical range of ravens has appeared to contract due the extirpation of wolves and bison during European colonization from the majority of the United States (Boarman and Heinrich 1999), but has recovered in many areas to the point that ravens are considered pests (e.g., Camp et al. 1993; Webb et al. 2004). This range recovery has been thought to have been facilitated by humans and their refuse that may increase winter food availability (Harlow et al. 1975; Camp et al. 1993; Boarman and Heinrich 1999; Webb et al. 2004). I examined this hypothesis in Jackson Hole, Wyoming specifically, because of the limited impact of humans afforded by Grand Teton National Park, and the dismantling of all refuse dumps within the Jackson Hole valley. I examined the prediction that ravens would not be subsidized by humans and that the raven population would be limited.

The population of ravens in Jackson Hole, Wyoming has been periodically studied for the past 57 years (Craighead and Craghead 1956; Dorn 1972*; Craighead and Mindell 1981; Craighead et al. 1987*; Dunk et al. 1997; Chapter 2), leading to the most complete, historical data set on Common Raven population ecology in North America. By examining nesting density data over time, I was able to find that a major population expansion occurred for the ravens sometime between 1948 and 1972, but the ecological factors supporting this increase were largely unknown. Since 1975, the nesting density of ravens in Jackson Hole has remained relatively stable, indicating that this population has likely reached carrying capacity for this area.

I did find that the nesting density of ravens in Jackson Hole is the second highest estimate recorded (1.9 pairs/10 km^2), while the mean productivity remained relatively low (1.14 fledglings/occupied nest; Chapter 2). When I examined the potential influence of a variety of demographic parameters (i.e., fledging date, brood size, hatching order, nest distance to the nearest human settlement, nearest neighbor distance) on both density and productivity, I found that raven density was positively related to indices of both human disturbance within the area (visitation to Grand Teton National Park) and winter food availability (annual elk harvest). However, I found no significant influence of any parameter examined on productivity (Chapter 2). From these findings, I suggest that human influence may have led to the over average nesting density of ravens in the Jackson Hole valley, but other parameters, such as density dependant selection, are regulating the current density level.

Given that I found low productivity and a dense population of nesting ravens, I investigated the post-fledging mortality of this population to determine if the young were experiencing low survivorship as well. Under dense conditions when a population is above or near carrying capacity, breeding pairs should produce fewer young, and the young should have decreased survivorship (Newton 1998). Conversely, in populations that are expanding, there should be increased production and survivorship. For two years, I followed the fledglings to departure from their natal areas. During this period, I found high survivorship of the young ravens (83%, *n* = 62; Chapter 4). Typically, in populations that are not increasing or decreasing in nesting density for a long time will remain at a relatively stable density and have constant rates of survivorship (Newton 1998). Such may be the case for this population of ravens. Considering that this population density has remained relatively stable and dense since 1975 (Chapter 2), reproductive rates may have dropped due to density dependant selection. Therefore, it may be advantageous for ravens to invest in maximizing survival of few young. For example, if a pair could raise two young to dependence, then it would be more cost efficient to produce two nestlings that would survive to independence, rather than producing four young initially, only to have two die after investing some resources into these young. Such conditions may favor a K-selection strategy, rather than a relatively r-selection strategy, which is typically exhibited by many raven populations (Ratcliffe 1997).

To examine this idea, I compared the variability in reproductive rates for both the population as a whole and for individual pairs across years. I found that the number of fledglings produced by the population varied less than expected, which provided some support for the hypothesis that the population has possibly maximized juvenile survival while minimizing waste investment. If the population was under selective pressure to expand or contract, the variation would likely be greater than expected. However, I only found limited evidence that this held true on the individual level (four pairs produced young with a significantly lower variance than expected, six did not differ from expected, and one was greater than expected). However, sample size was limited for analysis on the individual level.

Because my data suggested that this population has been at carrying capacity for at least three decades (Chapter 2), I wanted to test demographic parameters that have potentially kept this population from expanding further. Specifically, I wanted to examine potential effects that intra-specific competition, human augmentation, and food limitation during the breeding season had on juvenile survivorship. To do this, I first analyzed the relationship between nearest neighbor distance and survivorship, and found no pattern (Chapter 3). Conversely, I did find a positive relationship with juvenile survivorship and the distance of the nest to the nearest human settlement (Chapter 3). These findings supported the suggestion by Webb et al. (2004) that human augmentation may enhance populations of ravens by providing more available food resources. I suggest that while humans appear to facilitate increased juvenile survivorship, areas of low human density are needed to maintain source populations because of reduced human-related conflicts resulting in higher mortality rates in those areas (Chapter 3).

To test the potential effects of food resource limitation on the raven population in Jackson Hole, I investigated the factors correlated with juvenile departure from their natal territories. I predicted that if food was a limiting factor, then juveniles would leave natal sites early in years when food was scarce (Kenward et al. 1993). I found that juvenile departure seemed to be related to food, in that, during a year with abundant resources outside of the natal territories, the young left significantly earlier than a year where food resources appeared to be abundant across the valley (Chapter 4). These data supported the supposition that food may be the limiting ecological factor influencing the breeding population of ravens. Further evidence to support that food resources may be a limiting factor in juvenile survival, and therefore population expansion, was the finding of an relationship between juvenile departure date and brood size (Chapter 4; Figure 4.3; Kenward et al. 1993). If food is limiting in a territory, then the larger the brood, the earlier the family group would deplete the resources within and need to depart to maximize their chances of survival.

While the timing of the increase of nesting ravens in Jackson Hole is not precisely known (1950s – 1970s; Chapter 2), the positive relationship of visitor density in the valley and raven nesting density suggests that humans were influential in the origional population expansion. Further, the positive relationships between hunter success and nesting density (with a three year lag period; Figure 2.4) along with the positive relationship between nest distance to humans and juvenile survivorship (Chapter 2) suggest that this population increase may have been maintained by human influences.

Jackson Hole appears to be very well suited for a large population of nesting ravens because of low human density within most of the valley, and the protection afforded by Grand Teton National Park. Areas of low human density may be needed for healthy raven populations because of high levels of human persecution and increased anthropogenic deaths associated with ravens nesting near humans (Webb et al. 2004). Webb et al. (2004) documented relatively low survivorship of juvenile ravens prior to independence in California due to a high percentage of human caused deaths. While their California site and my study area both support relatively high nesting densities, my study area appears to be a source population because of high juvenile survivorship (Chapter 3). While the population studied by Webb et al. (2004) may be indicative of a sink population because of differential survival rates between the two populations (Table 3.4).

Because the evidence I collected supported that the population of ravens in Jackson Hole may limited by food, I suggest that the raven population was able to expand due to increased survivorship in the winter through human augmentation, in the form of an annual elk hunt (Figure 2.4). This increase in the winter food availability likely preceded an increase in survivorship of this population. As with many birds, the few months directly following juvenile dispersal from natal territories is a crucial time for the young of the year. With the annual elk hunt occurring shortly after the fledging-dependence period, juveniles are provided with an increased food supply until at least January, by which their food acquisition and flight skills are likely to have matured.

Another source of winter food subsidy in Jackson Hole could come from wolves (*Canis lupis*) in the area. However, while wolves are beginning to become relatively established within Jackson Hole because of recent reintroduction programs, the influence of these packs on wintering ravens is likely minimal due to the small number of packs (two or three) and large distances they travel in winter (M. Himmenez; U.S. Fish and Wildlife Service, pers. comm.). Besides as acting as a comparison for studies in areas dominated by humans, this study also acts as a reference site for further studies on the influence of expanding large carnivore populations on raven populations. In the near future, wolf populations within Jackson Hole are likely to expand and become a more permanent member of the ecological community.

I found that ravens may have exploited a human subsidy by utilizing waste left by hunters, and that this may have aided in maintaining an above-average density of ravens. I also suggest that the population expansion (Chapter 2) has not been facilitated by obvious human subsidies at least during the breeding season (e.g., refuse, powerlines). While it may appear counterintuitive that the ravens of Jackson Hole are gaining human augmentation since there is low human density in the area, there is a large influx of humans in the area that provide food subsidies related to elk hunting during the winter months. This large influx of humans in the backcountry where nests are located does not occur during the breeding season, and therefore poses little threat to the post-fledging survivorship of juvenile ravens. However, the increased food resources during this time may come at a key period and enhance survivorship of the ravens.

The ravens of Jackson Hole are providing an invaluable ecological service through scavenging of gut piles left by hunters and do not have the negative reputation typically associated with populations that utilize human refuse. Thus, the population has remained relatively undisturbed by humans. Therefore, my study provides baseline data on density, productivity, and post-fledging mortality of Common Ravens to which future comparisons can be made concerning both expanding human and large carnivore populations.

Documents Cited (Marked * in text)

Craighead, F. L., F.C. Craighead Jr., and **J.W. Tischendorf.** 1987. Stability of raptor communities over time. Craighead Environmental Research Institute, Moose, Wy.

Dorn, J. L. 1972. The Common Raven of Jackson Hole, Wyoming. M.S. thesis, University of Wyoming, Laramie.

Literature Cited

Boarman, W. I. and **B. Heinrich.** 1999. Common Raven (*Corvus corax*) *in* The Birds of North America, No 476 (A. Poole and F. Gill, eds.) The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Camp, R. J., R. L. Knight, H. A. L. Knight, M. W. Sherman, and **J. Y. Kawashima.** 1993. Food habits of nesting Common Ravens in the Eastern Mojave Desert. Southwest Naturalist 38: 163-165.

Craighead, J. J., and **F. C., Craighead, Jr.** 1956. Hawks, owls and wildlife. Stackpole, Harrisburg, Pennsylvania.

Craighead, F. C., Jr., and **D. Mindell.** 1981. Nesting raptors in western Wyoming, 1947 and 1975. Journal of Wildlife Management 45:865-872.

Dunk, J.R., R.N. Smith, and **S.L. Cain.** 1997. Nest-site selection and reproductive success in Common Ravens. Auk 114:116-120.

Harlow, R. F., R. G. Hooper, D. R. Chamberlin, and **H. S. Crawford.** 1975. Some winter and nesting season foods of the Common Raven in Virginia. Auk 92: 298-306.

Kenward, R. E., V. Marcstrom, and **M. Karlbom.** 1993. Post-nesting behavior in goshawks, *Accipiter gentilis*: I. The causes of dispersal. Animal Behaviour 46:365-370.

Newton, I. 1998. Population limitation in birds. Academic Press, NY.

Ratcliffe, D. 1997. The raven. Academic Press, San Diego.

Stahler, D., B. Heinrich, and **D. Smith.** 2002. Common Ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupis*, as a foraging strategy in winter. Animal Behaviour 64: 283-290.

Webb, W. C., W. I. Boarman, and **J. T. Rotenberry.** 2004. Common Raven juvenile survivorship in a human augmented landscape. Condor 106:517-528.