

IMPACTS OF INTRODUCED NORWAY RATS (*RATTUS NORVEGICUS*) ON
LEAST AUKLETS (*AETHIA PUSILLA*) BREEDING AT KISKA ISLAND,
ALEUTIAN ISLANDS, ALASKA DURING 2001 – 2003

by

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ABSTRACT

I quantified impacts of non-indigenous Norway rats on Least Auklets breeding at Kiska Island. Little direct evidence of rat predation was found in my productivity crevices, nevertheless hundreds of rat-predated Least Auklet adults, chicks and eggs were found at the auklet colony and in rat hoards. My estimate of adult Least Auklet survival from Kiska (0.88 in 2001 – 2002) was similar to values estimated by others. Yet in these years reproductive success was the lowest ever recorded (0.16 and 0.09) in the Aleutians. Norway rats foraging within the auklet colony were larger in size and showed increased reproductive activity than those foraging off the auklet colony. A simple population viability analysis, using current vital rate estimates, revealed that Least Auklets on Kiska are likely experiencing a rapid population decline. Continued monitoring and mitigation plans are required to further address the impacts of rats on auklets at Kiska.

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LIST OF ABBREVIATIONS AND SYMBOLS

AICc	Akaike's Information Criterion
AMNWR	Alaska Maritime National Wildlife Refuge
ANOVA	Analysis of Variance
E_i	Proportion of stage i birds breeding
F_i	Fecundity
G_i	Transition probability of moving from stage i to stage $i+1$
M_i	Mean fecundity at stage i
NIS	Non-indigenous species
p	Recapture rate
P_i	Stage i survival
PVA	Population Viability Analysis
QAICc	Quasi-Akaike's Information Criterion
USFWS	United States Fish and Wildlife Service
ϕ	Survival rate
λ	Population growth rate

CHAPTER ONE

INTRODUCTION AND OVERVIEW

1.1 BACKGROUND INFORMATION

1.1.1 Biological Invasions

A biological invasion can be defined as the expansion of any organism outside its previous geographical range (Williamson 1996, Vermeij 1996) and can be the result of an organism entering a previously unoccupied region through natural dispersion or introductions by other organisms (such as humans). Invasions are important in the evolutionary process, yet because of human activities, the frequency of invasions has increased (Williamson 1996). Not only have they become more frequent, but because humans have relatively easy access to remote locations, invasions of non-indigenous species (NIS) into areas where they could not have dispersed naturally (especially remote islands) have become common. However, biological invasions are not always deleterious, in fact, most natural biological invasions are not even successful (the invader does not become established in the new region; Williamson and Fitter 1996). Nevertheless, the cumulative effect of biological invasions that have succeeded is large (Williamson 1996), and island biotas have been especially hard hit with loss of biodiversity and even mass extinctions resulting from NIS (Steadman 1995, 1999, Steadman *et al.* 2002).

1.1.2 Vulnerability of Oceanic Islands to NIS

The theory of island biogeography states that invasions, colonization and the extinction of organisms on an island occur in synchrony and depend on the proximity of the source population and size of the recipient island (MacArthur and Wilson 2001). This theory has been criticized because of its hypothetical character and its limited applicability to NIS (Shrader-Frechette 2001). This is because most modern invasions result from the transportation of NIS by anthropogenic means, as opposed to dispersal and other natural routes of invasion. For successful invasion of remote islands, natural dispersal (i.e. dispersal through flight, or aided by the wind or a bird) by invading species would have to occur (Carlquist 1974).

An oceanic island can be defined as an island formed through vulcanism, tectonic uplift, or organic reef growth (Carlquist 1965). Oceanic islands have never had connections to continental landmasses, and thus tend to lack non-volant mammals, particularly herbivores and predators (Carlquist 1974, Paulay 1994). Biotas of oceanic islands are typically highly susceptible to NIS (Moors and Atkinson 1984, Atkinson 1985) because they have evolved with limited predation and thus lack effective defense mechanism against NIS (Greenway 1967).

1.1.3 Impacts of NIS

Examples of NIS and their impacts on native flora and fauna are numerous. The brown treesnake (*Boiga irregularis*) was introduced accidentally onto Guam about 1950 and has since been responsible for the extinctions of numerous native birds, bats, and

reptiles (Savidge 1987, Fritts and Rodda 1998). Other examples of NIS with far-reaching and varied impacts include honey bees (*Apis mellifera*) which may be interfering with endemic interactions among two floral species in Mauritius (Hansen *et al.* 2002), house mice (*Mus musculus*) which may pose a threat to indigenous invertebrates on Gough Island (Jones *et al.* 2003), terrestrial gastropods that decrease the diversity of native land snails and invertebrates on Pacific islands (Cowie 2001), lake trout (*Salvelinus namaycush*) that may cause the demise of Yellowstone cutthroat trout in Yellowstone Lake, Yellowstone National Park, Wyoming (Stapp and Hayward 2002), and Nile perch (*Lates niloticus*) that accelerated the decline of endemic fish and altered the food web structure in Lake Victoria, Africa (Kaufman 1992, Kitchell *et al.* 1997).

1.1.4 Vulnerability of Seabirds to NIS

Seabirds are particularly vulnerable to NIS because they are generally ground-nesting colonial breeders that are large and awkward on land and normally have few behavioural defenses against predators (especially terrestrial predators; Moors and Atkinson 1984). Many seabird species have experienced population declines due to NIS. The Ancient Murrelet (*Synthliboramphus antiquus*) colonies on Langara Island experienced drastic population declines due to introduced Norway rats (*Rattus norvegicus*; Bertram 1995, Bertram and Nagorsen 1995). The Xantus' Murrelet (*Synthliboramphus hypoleucus*) is an endemic breeding species on California's Channel Islands and islands off the coast of Baja California, Mexico, and has been experiencing population declines because of NIS throughout its range (McChesney and Tershy 1998).

In more serious cases seabirds are threatened with extinction because of NIS. Such is the case for the Dark-rumped Petrel (*Pterodroma phaeopygia*) in Hawaii and the Galapagos Islands, where introduced pigs (*Sus* spp.), mongooses (*Herpestes* spp.) and rats (*Rattus* spp.) are responsible for the endangerment of this species (Harris 1970, Coulter 1984, Harrison *et al.* 1984). In some cases, NIS are responsible for the extirpations and extinctions of avifauna. For example, the Guadalupe Storm-Petrel (*Oceanodroma macrodactyla*) became extinct from predation by introduced cats (Jehl and Everett 1985, McChesney and Tershy 1998).

1.1.5 Island Restoration

Notwithstanding the damage caused by NIS, the restoration of islands through eradication of NIS has been ongoing for many years with many successes. For example, Norway rats have been eradicated from many islands including islands in the Seychelles (Shah 2001) and Langara Island, British Columbia (Taylor *et al.* 2000). In New Zealand, 53 offshore islands and eight outlying islands have had at least one NIS eradicated successfully between 1920 and 2001 (Atkinson 2001). NIS eradication techniques are improving with time allowing successful eradications from larger islands to occur (Townes and Ballantine 1993). An alternative when eradication is not possible but native species are threatened with extinction are control programs (Thorsen *et al.* 2000). These programs for Black (*Rattus rattus*) and Norway rats on Ile de la Possession (Jouventin *et al.* 2003) and control of Black rats on Floreana Island, Galapagos Islands (Cruz and Cruz 1987), have both successfully decreased seabird mortality.

1.1.6 NIS in Alaska

Oceanic and coastal islands in Alaska have experienced many introductions including non-native foxes and rats (Bailey 1993 and Lensink 1984). Introduced Arctic foxes (*Alopex lagopus*) and Norway rats are known predators of seabirds and have been blamed for the disappearance of some species of seabirds from islands and have reduced the number of breeding seabirds on other islands (Atkinson 1985). Arctic fox eradication is ongoing in the Aleutian Islands and a new program to eradicate Norway rats is just beginning (AMNWR staff pers. comm.). In 1984, recommendations for seabird conservation were made by The International Council for Bird Preservation (ICBP) and included the elimination of alien species, protection from exploitation and research (ICBP 1984). This project, undertaken at Kiska Island, Aleutian Islands, Alaska, deals with these issues and aims to understand and quantify the impacts of introduced Norway rat as an NIS on this large oceanic island.

1.1.7 Rats as an NIS

The colonization of islands by rats outweighs all other causes of extirpations of island avifauna (Diamond 1985). Since 1600, 93% of the 93 species and 83 subspecies of birds that have gone extinct have been insular forms (King 1985). Rats are the most important introduced predator of insular avifauna, and more than 80% of large oceanic islands now have introduced rats (Shrader-Frechette 2001). Rats have exterminated at least 18 species and subspecies of birds, and another 40 are very rare as a result of rat predation (Roots 1976). However, the presence of rats on an island does not mean

certain devastation for avifauna. The impact of rats depends on the life-history of the native species, climate, ecology, and the occurrence of native predators on an island. Often, the presence of a native terrestrial predator on an island (e.g. land crabs), leads to the evolution of defense mechanisms in native fauna (e.g. nesting in locations inaccessible to predators) that may also be effective against introduced rats (Moors and Atkinson 1984, Atkinson 1985).

1.1.8 Norway rat

The Norway rat is a social, colonial and mostly nocturnal rodent (Olds and Olds 1979). Mean adult mass is 150 – 300 g, and mean total length (body plus tail) is 37 - 60 cm (Olds and Olds 1979, Moors 1990). They are omnivorous and their diet may include burrow and crevice-nesting birds (adults, eggs and nestlings), intertidal invertebrates, and vegetation (Moors 1990, Drever and Harestad 1998). Austin (1948) described the Norway rat as “a wanton, wasteful predator consuming but a small fraction of what it destroys” and Drever and Harestad (1998) suggested that Norway rats appear to exploit the highest quality and most readily available food source within their habitat.

Surplus (killing of prey without consumption) or excessive (killing of more prey than can be consumed) killing by carnivores (Kruuk 1972, Carbyn 1983) has been well documented for many species, including foxes (*Vulpes vulpes*) and spotted hyaenas (*Crocuta crocuta*; Kruuk 1972), *Canis* spp. (DelGiudice 1998, Patterson 1994 and Miller *et al.* 1985) and small predators, such as weasels (*Mustela nivalis*; Jedrzejewska and Jedrzejewski 1989) and mink (*Mustela vison*; Breault and Cheng 1988). Okansen *et al.*

(1985) described this behaviour along with food caching, or hoarding, as a hunting strategy for small generalist predators, like the Norway rat. These authors suggest that even partial consumption of a hoard can increase a predator's fitness, so surplus or excessive killing could be adaptive for predators that live in cold or dry environments, where hoards of prey items would not decay quickly. Hoarding behaviour in Norway rats was described by Bindra (1948a, b), Licklider and Licklider (1950) and Takahashi and Lore (1980), and may be related to the level of food deprivation or starvation (Fantino and Cabanac 1980, Cabanac 1985, Cabanac and Swiergiel 1989).

1.1.9 Least Auklet

With an estimated total population around 9 million, the Least Auklet is one of the most abundant seabirds in North America (Jones 1993a). Least Auklets are sexually monomorphic and socially monogamous with a high divorce rate (Bédard and Sealy 1984, Jones and Montgomerie 1991). They are characterized in all plumages by a dark back and white underparts that vary in the breeding season from white to heavily mottled (Bédard and Sealy 1984). With a mean adult body mass of 85 g and a total length of 12 – 14 cm, Least Auklets are the smallest alcid (Roby and Brink 1986, Jones 1993a). They are planktivorous and feed mostly on calanoid copepods (predominately *Neocalanus plumchrus*; Bédard 1969a, Roby and Brink 1986, Roby *et al.* 1986, Day and Byrd 1989, Piatt *et al.* 1990a, Hunt 1997, and Russel *et al.* 1999) and breed on the Aleutian Islands and other remote islands in the Bering Sea (Pearson 1936, AOU 1998). Breeding mostly occurs in large colonies in small rock crevices (Bédard 1969b, Knudtson and Byrd 1982).

Least Auklets have high breeding-site fidelity and a clutch size of one (Roby and Brink 1986, Gaston and Jones 1998). Because of their small size and nesting location, adults, juveniles and eggs are all vulnerable to rat predation. Dowding and Murphy (2001) warn that when a species' ability for reproductive compensation is low, as it is for Least Auklets, there may be cause for concern if productivity and adult survival are significantly diminished in the presence of NIS. Accordingly, the impact of introduced rats on Least Auklets at Kiska Island needed to be quantified.

1.2 STUDY SITE

1.2.1 Kiska Island

Initially called St. Stephen Island, Kiska Island (52°N 177°E) was discovered by the Russian explorer Chirikov in 1741 (Jochelson 1968). Located in the Alaska Maritime National Wildlife Refuge (AMNWR), Kiska is a remote oceanic island, lying more than 800 km from the nearest continental land masses. It is the second largest island in the Rat Islands group in the western Aleutian Islands, Alaska (Figure 1.1) and is approximately 39.8 km long and varies in width from 2.8 km to 11 km. Kiska Volcano (1232 m elevation) is the western-most active volcano in the Aleutian Island chain and dominates the northern tip of the island. Kiska is treeless and is characterized by tall grasses and ferns in low-lying areas, alpine heaths and meadows in higher inland areas, and sparse to no vegetation at higher elevations (Murie 1959). Insular avifauna are abundant on Kiska but there are no native terrestrial mammal species (Murie 1959).

Historically the Aleutian Islands were occupied by the Aleut people who had permanent and sustaining populations in the western Aleutians 2 – 3000 years ago (Laughlin 1980). In the late 1700s, Russians visited the Aleutians to hunt sea otters (Jochelson 1968) and in the 1800s Arctic foxes were introduced onto many of the Aleutian Islands for fur farming by the Russian – American Company (Murie 1959), including Kiska Island in 1835 (AMNWR staff pers. comm.). Since then, introduced foxes have been removed from most islands to restore avian breeding habitat and success (Byrd *et al.* 1994 and Ebbert 2000).

The Imperial Japanese Navy landed on Kiska Island in 1942 and began construction of a military base in Kiska Harbour, within days the Allied forces began air raids on Kiska and it was recaptured in 1943 (Perras 2003). Allied troops were stationed on Kiska Island until 1946 when the island was finally abandoned. Remnants of the Japanese and American bases including sunken and destroyed ships, submarines and airplanes and unexploded ordinance still litter the island and the coastal waters. Included in the refuse left behind were Norway rats (Murie 1959).

1.2.2 Sirius Point

Historically an auklet colony was located at North Head at the entrance to Kiska Harbour (Figure 1.1; Bent 1963). There is no longer an auklet colony at North Head, but at Sirius Point (52°08'N 177°37'E; Figure 1.2) a large Least and Crested Auklet (*Aethia pusilla*, *A. cristatella*) colony is situated on two lava domes located at the base of the northern slope of the volcano. The most recent of which formed during January 1962 –

September 1969, the last major eruption of Kiska volcano (Miller *et al.* 1998). The auklet colony covers a surface area of 1.8 square kilometers with a population estimated as 1.16 million Least Auklets (Day *et al.* unpublished report); more recently, the colony size has been estimated at 3 – 6 million birds (I. L. Jones unpublished data). This colony is the largest auklet colony located in the AMNWR (G. V. Byrd pers. comm.)

1.2.3 Lake District

Seven kilometers south of the auklet colony is a low-lying valley about 5 km wide that is dominated by three large lakes, one brackish and two freshwater (Lake District hereafter; Figure 1.2). No auklets breed or come ashore near the Lake District, but gulls, waterfowl and passerines breed there, and rats are abundant (H. L. Major and I. L. Jones, unpubl. data). In this study the Lake District has been used as a comparison for Norway rat population structure and body size with the Sirius Point auklet colony.

1.3 PURPOSE AND GOALS OF STUDY

1.3.1 Conceptual Framework

Lawton (1994) posed the question: ‘what do species do in ecosystems?’ and concluded that although there is no real answer to this question, some ecosystems do depend wholly on the presence of some key species. These species can be considered ecosystem engineers (organisms that provide habitat and resources that form the fundamental aspect of the ecosystem; Jones *et al.* 1994, 1997, Lawton 1994). Vitousek (1990) proposed that NIS can impact ecosystems in three ways, by changing resource

availability (e.g. nitrogen), energy flow, and by altering disturbance regimes.

Subsequently, Crooks (2002) added that NIS may act as ecosystem engineers by altering the environment which can have cascading impacts on the native biota. Nonetheless, the true effects of NIS on ecosystem structure and function have yet to be comprehensively described and understood.

In addition to decreasing numbers of breeding seabirds on islands, rats have been shown to significantly change the floristic composition on small islands (Palmer and Pons 2001). According to Vitousek's second effect, changing energy flow (Vitousek 1990), introduced rats on islands may be acting as ecosystem engineers. If rats are acting as an ecosystem engineer at Kiska Island they may not only be altering the Kiska Island ecosystem, but also the entire Bering Sea and Aleutian Island archipelago where Least Auklets play an important role. Thus, the presence of rats on Kiska may have impacts that are farther reaching and more negative than what is initially apparent.

1.3.2 Rationale and Questions

Lodge (1993) stated that the world's biota is rapidly being homogenized due to NIS introduced by human activities. There are numerous control and eradication programs ongoing around the world in an attempt to restore biological diversity. However, we are warned by Chapuis *et al.* (1994) and Atkinson (2001) to set out clearly defined goals for island restoration and that hasty action should be avoided, control measures are not necessarily successful in restoring biodiversity. The objectives of this study were to quantify the impacts of introduced Norway rat on the large Least Auklet

colony at Sirius Point, Kiska Island to determine whether or not a control or eradication program should be implemented. To accomplish this, three questions have been asked:

1. Does predation by Norway rats decrease auklet reproductive success and interannual survival at Kiska?
2. What is the distribution of Norway rats on Kiska Island and how does it differ between seasons?
3. Is the auklet colony at Sirius Point threatened with a population collapse, and if so what control measures are required to ensure the survival of this colony?

1.4 APPROACHES TO THE STUDY

1.4.2 Population Viability Analysis

Population viability analysis (PVA) is any analysis using demographic data to predict the future fate of a population; normally generating a probability of extinction (Boyce 1992, Marmontel *et al.* 1996, Coulson *et al.* 2001, and Caswell 2001). PVAs are a beneficial tool for assessing populations and making managerial decisions (e.g. Reed *et al.* 1998 and Horino and Miura 2000). However, PVAs are only as reliable as the data used to construct them (Doak *et al.* 1994, Taylor 1995, Coulson *et al.* 2001). Similarly, some studies have questioned the accuracy of PVAs and shown that there is typically a considerable amount of uncertainty in estimating extinction risk (Taylor 1995, Ludwig 1999, Coulson *et al.* 2001, Lindenmayer *et al.* 2003). In light of this, many studies suggest using PVAs for guidance to the efficiencies of different management options and

to address directions for further study (Possingham *et al.* 1993, Hamilton and Moller 1995, Ellner *et al.* 2002, Lindenmayer and Lacy 2002).

Perturbation analysis in PVAs is a popular analysis used to determine which population parameters, or vital rates are most important to the asymptotic properties of the population (i.e. population growth rate; van Groenendael *et al.* 1988). Two methods of accomplishing perturbation analysis are sensitivity analysis, the analysis of how sensitive one variable is to changes in another (Morris and Doak 2002) and elasticity analysis, or the proportional change of one variable to population growth rate (de Kroon *et al.* 1986; McDonald and Caswell 1993). These analyses give insight into what vital rates require further study and what management plans will best address those vital rates most important for conservation of a species (e.g. Crouse *et al.* 1987, Doak *et al.* 1994, Reed *et al.* 1998, Kelly and Durant 2000, Plissner and Haig 2000). The goal of the PVA in this study was to assess the viability of the current Least Auklet population and whether or not this varies with differing levels of rat management (ranging from controlling the rat population around the colony to the complete eradication of rats from the island). In this study I used a PVA to evaluate the potential impacts of Norway rats and various management options to preserve the Least Auklet colony at Sirius Point.

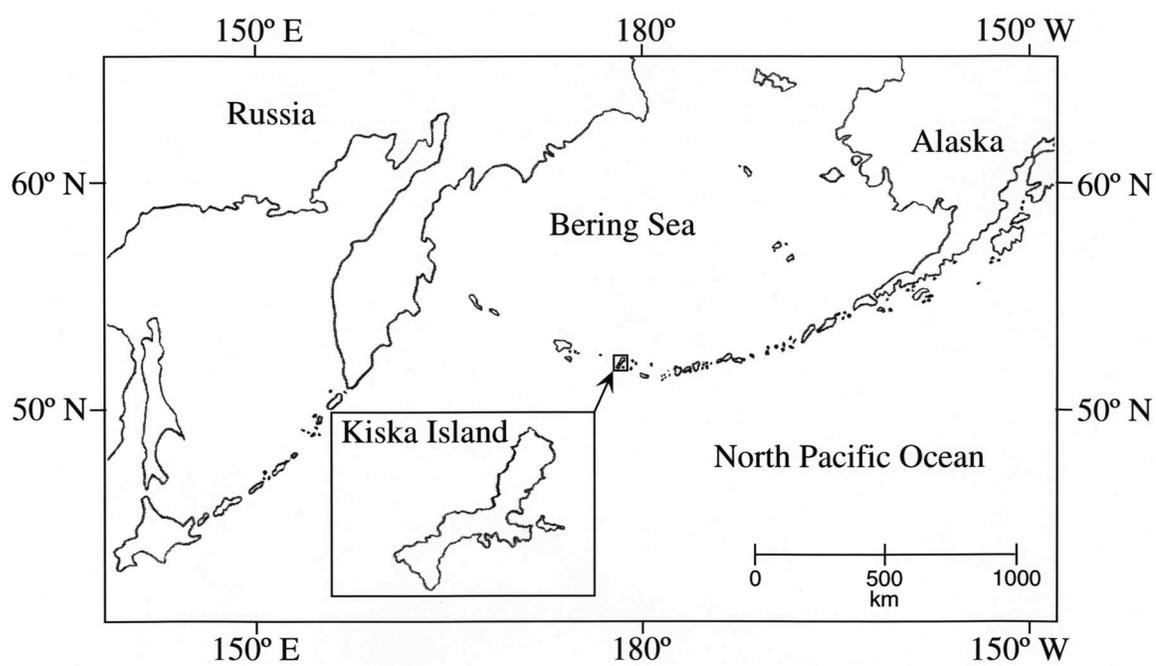


Figure 1.1 Map of the North Pacific showing the location of Kiska Island, Aleutian Islands, Alaska.

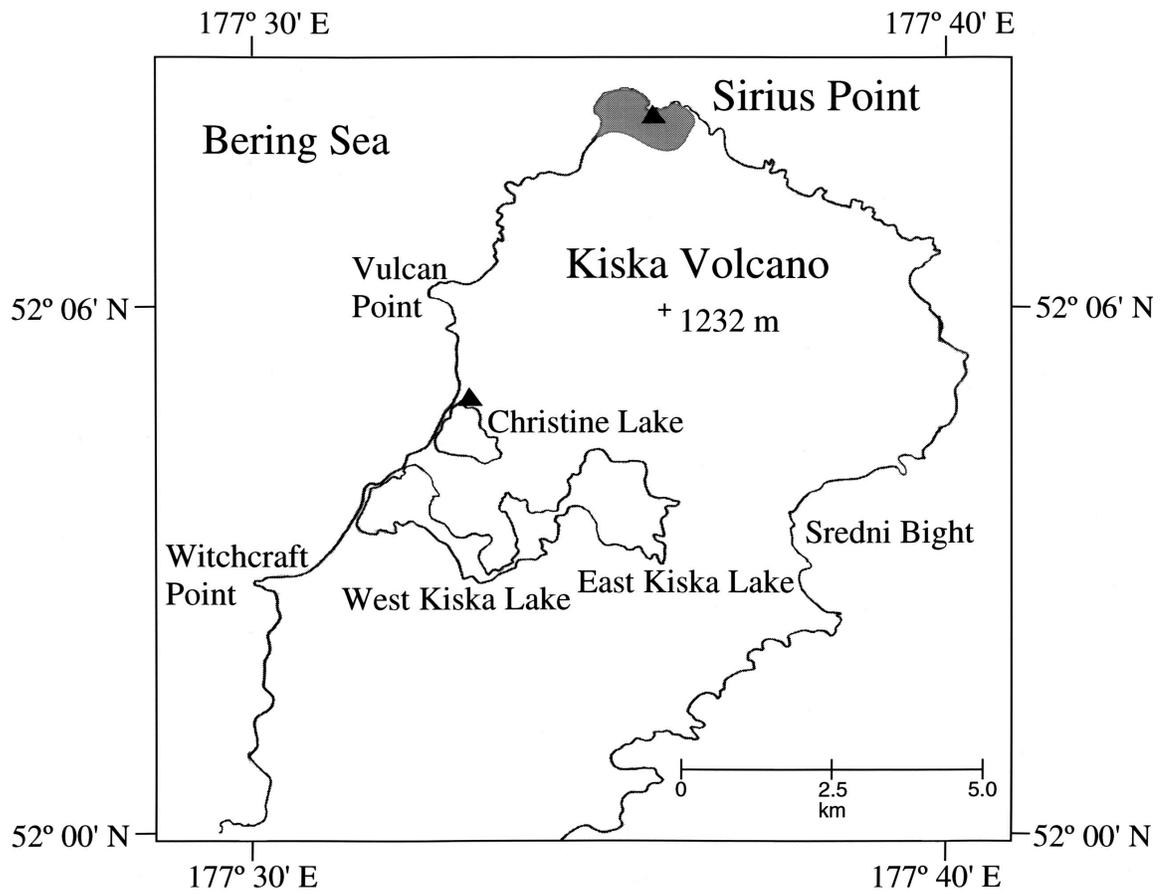


Figure 1.2 Map of the northern tip of Kiska Island showing the locations of Sirius Point and Christine, East and West Kiska Lakes (the Lake District).

CHAPTER TWO

ASSESSING THE EFFECTS OF INTRODUCED NORWAY RATS (*RATTUS NORVEGICUS*) ON REPRODUCTIVE PERFORMANCE AND SURVIVAL OF LEAST AUKLETS (*AETHIA PUSILLA*) AT KISKA ISLAND, ALASKA DURING 2001 – 2003

ABSTRACT

The Least Auklet breeding colony at Sirius Point, Kiska Island, western Aleutian Islands, Alaska, is the largest auklet colony on the Alaska Maritime National Wildlife Refuge and is one of the largest seabird breeding colonies in Alaska. This colony may be threatened by predation from introduced Norway rats that first appeared at Kiska during WWII. The goal of this study was to assess the impacts of rats on Least Auklets breeding at Sirius Point by comparing phenology, productivity (reproductive success from egg laying to chick fledging) and adult survival at representative study plots at Kiska during 2001 – 2003 to nearby rat-free auklet colonies (Buldir and Kasatochi Islands). At Sirius Point, Least Auklet chicks hatched significantly later than those at Kasatochi in 2001 and 2003 and those at Buldir in 2003. Furthermore, chicks on Kiska in 2002 and 2003 fledged later than those on both Buldir and Kasatochi. Least Auklet productivity at Kiska was significantly lower in 2001 and 2002 (0.16, 0.09; the lowest ever recorded for this species) than that measured on the other islands (0.52 – 0.61), except in 2003 when productivity at Kiska was actually higher (0.50) than that measured at Buldir (0.34).

Least Auklet chicks grew at a significantly slower rate at Kiska and fledged at a 14% lower mass than any measured at other colonies. Mean Least Auklet annual adult survival during 2001 – 2002 at Kiska (0.881 ± 0.033 , for the interval 2001 – 2002) did not differ significantly from either Buldir (0.853 ± 0.014 , mean for 1990 – 2003) or Kasatochi (0.893 ± 0.027 , mean for 1996 – 2003). One explanation for why the single adult survival estimate for Kiska was not lower than survival at colonies lacking introduced rats is because auklets at Kiska were marked late in the 2001 breeding season and thus escaped the most dangerous period for rat predation (incubation and brooding). If the low productivity of auklets at Kiska in 2001 and 2002 is a regular feature of this colony, a rapid population decline may be inevitable. Low productivity was consistent with predation and disturbance caused by rats, nevertheless it may also have been exacerbated by low prey availability for chick provisioning, many chicks were found that had presumably starved to death or were abandoned and succumbed to exposure. My information on survival was equivocal because of the single estimate of birds banded late in the breeding season, however it suggests that rat predation did not negatively impact survival in one year at one study plot. Further study is required to quantify annual variation in auklet productivity and annual adult survival over a longer time period.

2.1 INTRODUCTION

Predation by non-indigenous species (NIS), especially rats (*Rattus* spp), is the second most important cause of the endangerment, extirpation, and extinction of island birds after habitat destruction (King 1985). Currently more than 80% of major islands have introduced rats (Shrader-Frechette 2001) and approximately 54% of the extinctions of island birds have been attributed to rats (King 1985). Rats have been implicated in the declines of Ancient Murrelets (*Synthliboramphus antiquus*) at Langara Island (Bertram 1995), Xantus' Murrelets (*Synthliboramphus hypoleucus*), Ashy Storm-Petrels (*Oceanodroma homochroa*) and Cassin's Auklets (*Ptychoramphus aleuticus*) on Anacapa Island (McCheseny and Tershy 1998), and Dark-rumped Petrels (*Pterodroma phaeopygia*) in the Galapagos Islands (Harris 1970). However, direct evidence of rat predation has only been documented in a few cases, such as the predation of Laysan Albatross (*Phoebastria immutabilis*) at Kure Atoll, NW Hawaiian Islands by Polynesian rats (*Rattus exulans*; Kepler 1967).

Kiska Island (52°N 177°E) is the second largest island in the Rat Islands group in the western Aleutian Islands, Alaska and is part of the Alaska Maritime National Wildlife Refuge (AMNWR). A large auklet colony is located on the northern tip of the island at the base of Kiska volcano at Sirius Point (52°08'N 177°37'E). The auklet colony is situated on two lava domes with a surface area of 1.8 square kilometers and was occupied by as many as 3 – 6 million Least (*Aethia pusilla*) and Crested (*A. cristatella*) Auklets, in 2001 (I. L. Jones unpubl. data).

Norway rats (*Rattus norvegicus*) were accidentally introduced onto Kiska Island in the 1940s during military occupation of the island (Murie 1959). Norway rats are the largest of the *Rattus* species, and because of its large size may have a greater impact on seabirds than other *Rattus* species (Imber 1975). According to Atkinson (1985) birds nesting on or near the ground, or in burrows are vulnerable to predation by Norway rats, implying that seabird colonies at Kiska are likely to be impacted.

Least Auklets are an abundant, small, planktivorous seabird that breed colonially in rock crevices in the Aleutian Islands and other remote islands in the Bering Sea (Bédard 1969a, b, Knudtson and Byrd 1982, Jones 1993a). They are one of the most abundant seabirds in North America (Sowls *et al.* 1978). The smallest of the Alcids, Least Auklet adults weigh less than half the mass of adult Norway rats. Their small size and nesting location would appear to make Least Auklet adults, eggs and nestlings vulnerable to rat predation.

The auklet colony at Sirius Point is the largest on the AMNWR (G. V. Byrd pers. comm.). Accordingly, the goal of this study was to assess the impact of introduced rats on the Least Auklets at Kiska by comparing productivity and adult survival from Kiska to nearby rat-free colonies at Buldir Island (119 km to the west of Sirius Point) and Kasatochi Island (467 km to the east) where ongoing refuge monitoring studies are underway. I tested the hypothesis that if rats are present at Kiska then productivity and survival would be lower at Kiska than at rat-free islands due to predation and disturbance.

2.2 METHODS

2.2.1 Auklet Productivity

Least Auklet breeding crevices were located, marked and monitored once every four days from late May through early August during 2001 – 2003 to assess hatching, fledging and overall reproductive success. Hatching and fledging dates were estimated using the midpoint between crevice checks, laying dates were not estimated because most eggs had already been laid at the time of the first crevice check. These data were then compared to similar information collected by the U.S. Fish and Wildlife Service (USFWS) using the same protocol from rat-free Kasatochi and Buldir Islands, to determine the effects of rats on the productivity of auklets at Sirius Point. If a crevice failed it was carefully checked for the cause of failure including signs of rat predation on adults, eggs and nestlings.

At Kiska, productivity monitored crevices (190 in 2001, 195 in 2002, 201 in 2003) were checked on three study plots that were believed to be representative of the variability in habitats at the Sirius Point auklet colony. The first productivity study plot ‘New Lava’ (centered at 52°08.038'N 177°35.780'E, Figure 2.1) was located on the top and east side of the most recent lava dome, which was created during the last eruption of Kiska volcano during 1965-69 (Miller *et al.* 1998). All of the crevices on this plot were within 60 m of the coastline, at an elevation of 25 - 30 m in an area sparsely vegetated with lichens. The second productivity study plot ‘Old Lava Low’ (centered at 52°07.813'N 177°35.724'E, Figure 2.1) was located in the valley between the 1965-69 lava dome and Bob’s Plateau (52°07.803'N 177°35.731'E). All of these crevices were

within 520 m from the coast at an elevation of 190 m. This second plot was in an area densely vegetated with *Carex* sp., *Calamagrostis* sp. and fern overgrowing basalt blocks. The third plot 'Old Lava High' (centered at 52°07.704'N 177°36.139'E, Figure 2.1) was located at the top of Bob's Plateau close to the base of a steep talus slope of blocky lava on the northern face of Kiska volcano. These crevices were within 800 m of the coast at an elevation of 180 m. The Old Lava High productivity plot was moderately vegetated with *Carex* sp. and ferns. Long term monitoring of auklet survival and productivity is ongoing at rat-free Main Talus, Buldir Island (52°23.266' N 175°55.029' E, 10+ years) and Thundering Talus, Kasatochi Island (52°10.751' N 175°31.183' W, 7 years) as part of a long-term seabird monitoring program by AMNWR. Productivity at the three Kiska study plots was compared to productivity at samples of crevices widely scattered over the auklet colonies at Buldir and Kasatochi. A two-way analysis of variance (ANOVA) was used to assess whether mean hatch and fledge dates (Table 2.1) varied significantly between the three islands (Kiska, Buldir and Kasatochi Islands) and between the three years (2001 – 2003). T-tests were then used to look at the differences between islands adjusting the significance criteria using Bonferroni correction of the p-value ($p\text{-value} \leq \alpha = 0.05 / 3$).

2.2.2. Chick Growth and Breeding Chronology

To evaluate if the nutritional requirements of the chicks at Kiska were being met and were similar to those at other Least Auklet colonies, chick growth was monitored during the 2002 and 2003 breeding seasons. Chicks were measured once every four days

from hatching until fledging in 40 crevices found near the end of incubation in 2002 and 2003. Chick age was estimated at time of discovery: where if a chick was wet it was presumed to be one day; dry but wobbly, two days; and dry, alert and coordinated, three plus days. In order to identify any differences in the chick growth rate of the birds at Kiska, measurements of mass, tarsus, and wing chord length were taken and were compared to similar chick growth measurements from other colonies. When a chick was found dead similar measurements were taken and the crevice and chick were examined closely to determine the cause of death.

Using the methods outlined by Ricklefs (1967) chick growth measurements were fit to a logistic growth curve. Because the residuals of the linear regression were not normal, a bootstrap estimate was used to calculate the growth rate at Kiska. The mean and maximum instantaneous growth rates were then compared to those found on St. Lawrence and the Pribilof Islands by Sealy (1973), Piatt *et al.* (1990a) and Roby and Brink (1986) where similar methods were used to collect and analyze the data. The 2002 chick growth data was not fit to the logistic growth curve because there were not sufficient data available. Growth rates of mass and wing chord length were also calculated for 2002 and 2003 by finding the mean slope of the regression line for each bird measured at least twice during the linear growth phase (6 – 18 days old). These data were then compared to those measured on Kasatochi Island in 2002 and 2003 (USFWS AMNWR unpubl. data), using Bonferroni correction of the p-value ($p\text{-value} \leq \alpha = 0.05 / 2$).

2.2.3 Adult Survival

Auklets were captured for colour marking using noose carpets set on the colony surface within a single 50 m² (surface area) study plot (centered at 52°08.038'N 177°35.780'E) near the New Lava productivity study area, Sirius Point, Kiska Island. Noose carpets were used because they are believed to randomly select breeding and non-breeding auklets from the population (Jones 1992a, b, 1993b). Each captured adult auklet was given a numbered stainless steel leg band and a unique combination of three Darvik plastic colour bands. I could not determine the sex or precise age of individuals in the sample, nevertheless sub-adult birds (two year olds, identified by criteria described by Jones 1993b; Jones and Montgomerie 1992) were not colour banded and not included in the survival analysis. Survival data from Kiska were combined with similar data from study plots at Buldir (52°22.577'N 175°54.288'E; Jones *et al.* 2002) and Kasatochi (52°10.813'N 175°31.365'W; Barton and Lindquist 2003) Islands.

Resighting of colour marked auklets were made daily (except during the most severe weather conditions) during mid-May to early August (Buldir 1990 – 2003; Kiska 2001 – 2003; Kasatochi 1996 – 2003) encompassing the birds' laying, incubation and chick-rearing periods. Birds attending the study plot were observed from a plywood blind during their morning and evening activity periods (0900h – 1400h; 2200h – 0030h) and the colour band combinations of all marked individuals present were recorded.

Local adult annual survival (ϕ) and recapture (p) rates were estimated using methods described in Lebreton *et al.* (1992) and Burnham and Anderson (1998), with the program MARK (White and Burnham 1999). I began by defining a global model

(Burnham and Anderson 1998, Anderson and Burnham 1999a) where recapture rates were allowed to vary over time (i.e., the years of this study) and between islands (Buldir, Kiska and Kasatochi). Since the marking technique used is known to catch both non-breeding and breeding adult birds, I expected that some individuals ('prospectors') might show lower site fidelity, and hence lower local survival rates, after their first capture (Pradel *et al.* 1997, Prévot-Juilliard *et al.* 1998, Bertram *et al.* 2000). To account for this hypothesis, survival rates in the year after the initial capture were modeled independently of survival in subsequent years. Structurally, this approach is similar to age-based models (Lebreton *et al.* 1992). In this model, apparent survival after first year of capture is a combined estimate of true survival and permanent emigration rates (because the sample of marked individuals includes transient birds), while survival in subsequent years (of resident individuals) is a better approximation of true survival (Pradel *et al.* 1997).

In summary, the global model incorporated both a group effect (island) and time dependence (year) in both the survival and recapture models. The goodness-of-fit of this global model to the data was determined using a parametric bootstrap approach, based on 100 bootstraps, described in Cooch and White (2001). From these bootstraps, the mean of the model deviances and \hat{c} were extracted. \hat{c} is a measure of over-dispersion, or extra-binomial variation, in the data. It arises when some model assumptions are not being met, such as heterogeneity in survival or recapture rates among individual animals (Burnham and Anderson 1998). In addition, I tested the goodness of fit of a two-age class model with a group effect (island) in the survival model and both a group effect (island) and time dependence (year) in the recapture model; and a random effects model

(where both within island variance and between island variation are included in the assessment of the confidence intervals) with both a group effect (Kiska, random effects Buldir and Kasatochi) and time dependence (year) in the survival model, and both a group effect (island) and time dependence (year) in the recapture model. Similar notation to Lebreton *et al.* (1992) was used, where the parameterization of each class was explicitly described (a1 = first age class, a2 = all subsequent age classes); the two-age model was $\phi(a1, a2*\text{island}), p(\text{island}*year)$.

The candidate models were restricted to the global model, plus a series of reduced parameter models, including Cormack-Jolly-Seber (Lebreton *et al.* 1992) models (time and group dependent, no age structure) and a random effects model for Buldir and Kasatochi, to assess whether age-structure was appropriate. I used the approach described by Lebreton *et al.* (1992) by first modeling recapture rates to determine the best structure for recapture rates and then modeling survival rates.

Relationships among factors were indicated using standard linear model notation. Model selection was based on comparison of the Quasi-Akaike's Information Criterion (QAICc), where the models with lowest QAICc values suggest the best compromise between good fitting models and models with relatively fewer explanatory variables (i.e. parsimonious; Burnham and Anderson 1998, Anderson and Burnham 1999a). QAICc, instead of Akaike's Information Criterion (AICc) was used to rank models, as an acknowledgment of the extra-binomial variation in the data set, represented by c-hat (Burnham and Anderson 1998, Anderson and Burnham 1999b). QAICc weights were

also calculated, as they provide a relative measure of how well a model supports the data compared with other models (Anderson and Burnham 1999a).

2.3 RESULTS

2.3.1 Auklet Productivity

Least Auklet breeding chronology varied among years (2001 – 2003) and islands (Kiska, Buldir and Kasatochi); (Table 2.1). A two-way ANOVA comparing hatch and fledge date to island (Kiska, Buldir and Kasatochi) and year (2001 – 2003) revealed in both cases a significant interaction term ($p\text{-value} > 0.001$) suggesting that the differences between islands depends on years. There were no significant differences in hatch date among the three colonies in 2001 ($p\text{-values} \geq 0.203$) but in 2002 and 2003 the hatch dates at Kiska were significantly later than those measured at Kasatochi and Buldir Islands ($p\text{-values} < 0.001$). Fledging dates at Kiska were also significantly later than Kasatochi in 2001 and 2003 ($p\text{-values} \leq 0.002$), but not 2002 ($p\text{-value} = 0.053$), and significantly later than those measured at Buldir in 2003 ($p\text{-value} < 0.001$), but not 2001 and 2002 ($p\text{-values} \geq 0.019$).

Hatching and fledging success and productivity (Figure 2.2) varied among islands and years throughout this study (Table 2.2). Hatching success at Kiska was not significantly different from either Kasatochi or Buldir in 2001 and 2003 ($p\text{-value} \geq 0.058$), but was significantly lower at Kiska in 2002 ($p\text{-value} \leq 0.002$). Fledging success and productivity at Kiska in all three years was significantly lower than that measured at Kasatochi ($p\text{-values} < 0.001$;) and Buldir ($p\text{-values} < 0.017$) Islands. Within islands,

among years, hatching and fledging success and productivity differed significantly at Kiska and Kasatochi (p-values ≤ 0.005), where the highest successes occurred in 2003 and the lowest in 2002 (Table 2.1). In contrast, hatching success on Buldir Island did not differ significantly across years (p-value = 0.547), whereas fledging success and productivity did (p-values ≤ 0.004) and were highest in 2002 and lowest in 2003 (Table 2.2).

Productivity was extremely low at Kiska during 2001 (0.13) and 2002 (0.09), the lowest productivity recorded for any island in any year (Table 2.2). The most frequent cause of breeding failure at Kiska in these two years (2001 and 2002) and at Kasatochi in 2003 was unexplained chick death, normally occurring during the first week after hatching (45% and 35% at Kiska in 2001 and 2002; and 10% at Kasatochi in 2003 of the total number of crevices; Table 2.2). The second most frequent cause of breeding failure at Kiska in 2001 and 2002 was the disappearance of chicks from their nest crevices without a trace (17% of the total number of crevices in both years; Table 2.2). This was also the most frequent cause of breeding failure at Kiska in 2003, Kasatochi in 2001 and 2002 and Buldir in 2001 – 2003 (~20% of the total number of crevices; Table 2.2).

2.3.2 Chick Growth and Breeding Chronology

At Kiska in 2002 Least Auklet chicks grew extremely slowly and out of 41 marked crevices used to measure chick growth only two chicks survived until fledging age. I am concentrating on data collected in 2003 because there were not sufficient data available from 2002. Least Auklet chicks increased steadily in mass until approximately

20 days of age (Figure 2.3) in 2003. Least Auklets fledge when they are approximately 25 days old, and at this time should be at or above adult body mass (Roby and Brink 1986, Piatt *et al.* 1990a). At Kiska in 2003, Least Auklets fledged around 29 days of age and had a body mass of 73.2 g (standard deviation of 9.8, $n = 11$), which was not significantly different (p -value = 0.3) than adult body mass (Table 2.3) as measured on the Kiska banding plot between 2001 – 2003. Wing chord length increased steadily throughout the nestling period at Kiska (Figure 2.4). Similar to mass, when Least Auklets fledge their wing chord length should be at or near adult wing chord length (Roby and Brink 1986, Piatt *et al.* 1990a). Least Auklet wing chord length at fledging was 83.5 mm (standard deviation 6.8, $n = 11$) at Kiska in 2003, which is significantly shorter (p -value = 0.025) than adult wing chord length (98 mm, standard deviation 2.3, $n = 283$) as measured on the Kiska banding plot in 2001 – 2003.

Least Auklet chick growth rates from Kiska in 2003 were approximately 50 – 60% lower than all other estimated growth rates from previous studies (Table 2.3). In addition the lowest asymptotic and fledging masses measured were all from Kiska (Table 2.3). A bootstrap estimate was used because regression analysis of the chick growth rate measured at Kiska in 2003 revealed non-normal errors.

Least Auklet chick growth rates were also compared to those measured at Kasatochi Island during 2002 – 2003 (Table 2.4). The growth rates for mass and wing chord length were significantly lower at Kiska in 2002 (p -values < 0.002) but not in 2003 (p -values > 0.041).

2.3.3 Adult Survival

The data provided a good fit to the global model with three groups (islands) and time dependence (year) in both survival and recapture rates. The c -hat as calculated by the parametric bootstrap goodness of fit test, was 1.98, which suggests some extra-binomial variation. This c -hat was used to adjust all QAICc values.

The best model in the final candidate model set was the random effects global model with survival and recapture rates differing between island and year. This model ($\phi((\text{Random effects island}) * \text{year}) p(\text{island} * \text{year})$) was 3332 times ($0.9996 / 0.0003$; Table 2.5) better supported by the data than next most parsimonious model. The second best model included groups (islands) and time (years) in the survival and recapture rates ($\phi(\text{island} * \text{year}) p(\text{island} * \text{year})$; Table 2.5). From the best model, the survival rate at Kiska in 2001 (0.8814 ± 0.0332) was not significantly different than that from Buldir (0.8526 ± 0.0144 ; p -value = 0.212) and Kasatochi (0.8934 ± 0.0266 ; p -value = 0.390; Appendix A). However, Least Auklet adult survival varies across both island and year in the Aleutians (Figure 2.5).

2.4 DISCUSSION

Generally seabirds are a long-lived species that nest in areas safe from mammalian predators. As a long-lived species they tend to have low fecundity in a given year and normally outlast periods of unfavorable feeding conditions. However, in rare circumstances seabirds may be limited by the amount of food available and experience a population decline, such as the Atlantic Puffins (*Fratercula arctica*) on St. Kilda

(Boddington 1960). If food availability determines survival and productivity in auklets I would predict that in years of poor oceanographic conditions Least Auklet adult survival and productivity would be decreased.

Rattus species have been implicated in the declines of many breeding seabird species (see Atkinson 1985). Yet as in my study at Kiska, there was limited direct evidence isolating rat predation as the clear cause of population declines. There was however, indirect evidence of rat predation and disturbance affecting the auklet populations on Kiska. Norway rats at the Sirius Point breeding colony were found to be larger in overall size, exhibit increased breeding activity and Norway rat sign was more abundant when compared to those found off the auklet breeding colony, suggesting rats are subsidizing their diet with auklets at Sirius Point (Chapter 3). If auklet adult survival and productivity are determined by rats I would predict that in the presence of rats Least Auklet adult survival and productivity would be decreased. Furthermore, in years of poor oceanographic conditions and in the presence of rats I would predict that Least Auklet adult survival and productivity would be drastically reduced.

2.4.1 Auklet Productivity

During 2001 – 2003 Least Auklet productivity was quantified at Kiska Island. With only three years of data and extreme intra-annual variation, definitive conclusions cannot be drawn concerning the impacts of Norway rats. Comparisons with long term monitoring data from rat-free Buldir and Kasatochi Islands suggests that rats were implicated in the near reproductive failure at Kiska during 2001 and 2002. Monitoring

on the productivity study plots at each island includes peering into crevices with a light, increasing disturbance on the auklets breeding in these crevices. This monitoring technique may bias my ability to measure actual reproductive success in the absence of human disturbance, which has been shown to decrease auklet productivity (Piatt *et al.* 1990a). Only crevices that are near the surface of the colony and that can be viewed in their entirety can be monitored. I do not know whether birds that nest in these surface crevices are indicative of birds nesting in deep crevices at the colony. However, because similar methods are employed at the three monitoring locations (Kiska, Buldir and Kasatochi) my estimates are comparable and if the rats have a noticeable effect on the birds at Kiska I should have been able to detect it using these methods.

In both 2001 and 2002 at Kiska, Least Auklet productivity was the lowest ever recorded for this species, suggesting something unique to Kiska Island was the cause (e.g. rats). Yet, in 2003 productivity returned to what is considered normal for the species (0.5, Knudtson and Byrd 1982, Roby and Brink 1986, Piatt *et al.* 1990a) even though rats were still present on the colony. One hypothesis concerning the large fluctuation in productivity at Kiska is the variable abundance of rats early in the breeding season. If rats are more abundant early in the breeding season when adult auklets are most vulnerable to predation (during incubation and brooding) then I would expect to see reduced auklet reproductive success. Similarly, if rat abundance was low early in the auklet breeding season, as it was believed to have been in 2003 with comparison to 2002 and 2001 (estimated using the abundance of rat sign, Chapter 3) then I would expect auklet reproductive success to be not as significantly impacted. A detailed study of rat

abundance and distribution has not been performed at Kiska and I have little direct evidence of rat predation in my productivity study crevices. However, anecdotal evidence does suggest that rats (as indicated by the presence and abundance of their sign) did vary in abundance throughout this study.

There was little direct evidence that breeding failure at Kiska resulted from rats alone during 2001 – 2003. Only six crevices were found with obviously rat predated eggs (all found in 2003), one obviously rat predated chick (found in 2001) and one obviously rat predated adult (also in 2001). However, clear sign of rat activity was not expected even with severe rat predation occurring, because rats normally move their food for hoarding or consumption. The most frequent confirmed cause of breeding failure was due to chick death, which normally occurred within a week of hatching at Kiska in 2001 and 2002. In 2003, the most frequent cause of reproductive failure at Kiska was chick disappearance, which was the most likely cause of reproductive failure on Buldir and Kasatochi Islands during 2001 – 2003. Both of these kinds of breeding failure are consistent with rat disturbance or predation, but could be explained by other causes such as a food shortage or uncommonly wet or cold weather. There was little direct evidence of rat predation and although reproductive success at Kiska was extremely low in 2001 and 2002, there were years such as 2003, where productivity was comparable to that at similar rat-free islands. Rats are present only at Kiska, and only at Kiska did auklets suffer near complete reproductive failure in a combined total of 25 years of monitoring at the three islands.

Nevertheless, Kiska is also the largest colony of the three sites monitored and reproductive failure could have been partly attributable to a density dependent driven local food shortage caused by the large number of birds feeding nearby Kiska Island. Food shortage provides an alternative explanation for breeding failure at Kiska because it is consistent with the observed deaths of many small chicks presumably due to exposure and starvation. Previous work has shown that auklet adult survival varies with large-scale oceanographic conditions (Jones *et al.* 2002). Similarly, during periods of low oceanographic productivity there will be less food available for nestlings leading to a decrease in auklet productivity. However, it is presumed that Least Auklets from Kiska and Buldir are feeding at the same location, at Buldir Reef, approximately half way between Buldir and Kiska Islands. If this is in fact the case, then the observed average breeding success at Buldir in 2001 and 2002 would suggest that a food limitation is not occurring and thus was not the limiting factor for the birds at Kiska in these years. In addition, even though chick death at Kiska is consistent with starvation or exposure no lab post mortems were performed and the true cause of death remains unknown.

2.4.2 Chick Growth and Breeding Chronology

Breeding chronology and productivity varied significantly among island and year throughout this study, but at Kiska, Least Auklets tended to hatch and fledge later than at the other two islands and had lower hatching, fledging and overall productivity. Virtually all productivity and chick growth crevices failed in 2002, providing very little chick growth data. However, in 2003 half of the productivity and chick growth crevices at

Kiska produced a fledgling. This resulted in reliable chick growth data from only one year (2003), which compared to 2001 and 2002 was an extremely good year for productivity at Kiska and may not have been an accurate estimate of chick growth during the 'normal' productivity years.

As reported in studies by Piatt *et al.* (1990a) and Roby and Brink (1986), Least Auklets grow in mass and wing chord at a steady rate until approximately 20 days of age, when growth levels off and chicks fledge at or above adult body mass and wing chord length. In contrast Least Auklet chicks at Kiska fledged below adult wing chord length and grew at a slower rate, had a lower asymptotic and fledging mass when compared to all other Least Auklet chicks measured at other Alaskan colonies. In addition, Least Auklets adults on Kiska had a lower body mass than any other measured in Alaska.

Studies have found that when eggs are laid earlier in the breeding season, chick growth rate and fledging mass are higher than those measured from eggs laid later in the breeding season (Birkhead and Nettleship 1981, Ydenberg *et al.* 1995). This trend was apparent in this study, with Least Auklets at Kiska having a later hatch date, slower growth rate and overall lighter fledging mass in comparison to other studies. If this is indeed the case, the reason for later reproductive activity at Kiska needs to be assessed. I propose three hypotheses concerning why this trend is occurring at Kiska. First, there is evidence that Norway rats kill and hoard large numbers of auklets during the laying period, likely killing mostly older and more experienced birds. This could have led to birds that arrived later at the Sirius Point auklet colony being able to find a suitable nesting crevice and breeding in higher numbers than at other islands. This would lead to

an increased proportion of inexperienced birds breeding at this colony resulting in decreased reproductive success, as these inexperienced birds may have a difficult time providing the quantity and quality of food required by the chicks to grow at the ideal rate. Second, because Kiska is one of the largest Least Auklet breeding colonies in Alaska, I have hypothesized that in years of poor oceanic productivity this colony will do drastically worse than the smaller colonies because of increased density dependent food shortage. Ashmole (1963) suggested that large seabird colonies locally deplete the food supply resulting in a food shortage halo around the colony. If this was the case then it is possible that in years when a local food shortage halo is present around Kiska, Least Auklets would be forced to feed farther away and may not be able to provide their chicks with an equal amount of nourishment as those birds from the other colonies. Finally, according to Jones and Montgomerie (1991) Least Auklets have a high divorce rate that increases with unsuccessful breeding attempts. They also showed that auklets that divorced and found a new mate were in worse condition than those that remained with their mate from the previous year, had a significantly later laying date and an increased chance of breeding failure. Both the activities of rats and poor oceanographic conditions for foraging near Kiska would create increased divorce rates by reducing auklet reproductive success and survival, further decreasing productivity by increasing the number of new unfamiliar breeding pairs. Further study is required to assess these three hypotheses before any of them can be accepted or rejected.

2.4.3 Adult Survival

Adult survival at Kiska over the period early July 2001 to early July 2002 which included a breeding season when most adults experienced breeding failure and returned to sea early, at one study plot on the new lava was estimated to be 0.8814. This rate is close to the mean survival rate at Buldir (0.8465 ± 0.010) and Kasatochi (0.8863 ± 0.008) over the previous decade, where survival rates included the active breeding seasons without reproductive failure. At Kiska adults were marked during mid to late June and early July in 2001 and most departed the colony shortly after, as most crevices failed close to the time of hatching. These birds were resighted starting in late May 2002, therefore, birds killed by rats during the incubation period in 2001 (when the adults are most vulnerable) were not accounted for in this first estimate of survival. The high interannual variation in survival in auklets makes it difficult to interpret the significance of the single survival estimate from Kiska. Several more years of estimation are required before any generalizations can be made about annual adult survival rate at Kiska and whether rats might be affecting this important demographic parameter. Nevertheless, the single survival estimate for 2001 – 2002 at Kiska at least suggests that rats were not having a drastic impact on adult Least Auklet survival during that time period. Like other demographic parameters, adult survival might be expected to vary across a large colony, so I should be concerned about any estimate based on a single study plot. I believe the survival plot at Sirius Point was representative of the colony in general because it is centrally located in an area of average density of nesting auklets, where signs of rats (droppings, predated adults and chicks) were prevalent.

Auklet adult annual survival varied across Aleutian Islands and years, similar to productivity. Explanations for the variation in survival include size of colony, local and regional oceanographic conditions (Jones *et al.* 2002), local predator populations (e.g. Glaucous-winged Gull *Larus glaucescens*, Peregrine Falcon *Falco peregrinus* and Bald Eagle *Haliaeetus leucocephalus*), and introduced predators such as rats. In most cases it would be assumed that an introduced predator would have a negative impact on adult survival. However, under some conditions the impacts of an introduced predator may not be immediately reflected with reduced adult survival.

Breeding efforts may be terminated if reproductive effort in one year will decrease survival or reproductive output in future years (Williams 1966). Least Auklets breeding at Kiska may not have exhibited decreased survival because of their abandonment during both the late incubation and early brooding periods of 2001. In effect, disturbance caused by introduced rats could explain increased auklet survival if as a result adults left the breeding colony early without having experienced the energetic stress and risk associated with breeding at Sirius Point. Without this reproductive cost, I hypothesize that adult Least Auklets breeding at Kiska could exhibit an apparently normal or even increased survival in the face of rat activities.

In summary, the data indicate possible impacts of rats on auklet productivity at the large colony at Sirius Point. Further years of data are required to account for the observed high inter-year variation in productivity, and to robustly quantify adult survival. Further studies need to be done to properly assess impacts of introduced Norway rats on

auklets and their more general consequences to the terrestrial ecosystem of Kiska Island as a part of management or mitigation plans.

Table 2.1 Summary of mean Least Auklet hatching and fledging dates at Kiska, Kasatochi and Buldir Islands in 2001 – 2003.

	Kiska			Kasatochi ^a			Buldir ^a		
	2001	2002	2003	2001	2002	2003	2001	2002	2003
Mean Hatch Date	27 June	6 July	3 July	28 June	27 June	25 June	26 June	25 June	27 June
(n)	(150)	(124)	(160)	(50)	(68)	(35)	(30)	(13)	(14)
Mean Fledge Date	26 July	31 July	30 July	28 July	26 July	23 July	25 July	25 July	26 July
(n)	(11)	(4)	(52)	(53)	(46)	(28)	(33)	(30)	(28)

^aUSFWS AMNWR unpublished data

Table 2.2 Summary of Least Auklet productivity and known causes of breeding failure at Kiska, Kasatochi and Buldir Islands in 2001 – 2003.

	Kiska			Kasatochi ^a			Buldir ^a		
	2001	2002	2003	2001	2002	2003	2001	2002	2003
Number eggs n(a)	190	195	201	85	97	110	65	50	83
Number hatched (b)	149	127	164	65	80	95	55	43	75
dead adult	1	0	2	0	0	0	0	0	0
egg abandoned	17	27	19	11	14	5	5	3	4
egg broken	1	10	1	5	1	6	0	0	2
egg disappeared	21	30	9	4	2	4	5	4	2
egg displaced	1	1	0	0	0	0	0	0	0
egg predated	0	0	6	0	0	0	0	0	0
Number fledged (c)	31	18	100	47	50	80	36	30	28
chick disappeared	32	33	40	14	20	4	15	10	39
dead chick	86	69	20	4	10	11	4	3	8
dead chick (injured)	0	6	5	0	0	0	0	0	0
dead chick (predated)	0	1	0	0	0	0	0	0	0
Hatching success (b/a)	0.78	0.65	0.82	0.77	0.83	0.86	0.85	0.86	0.90
Fledging success (c/b)	0.21	0.14	0.61	0.72	0.63	0.84	0.65	0.70	0.37
Productivity (c/a)	0.16	0.09	0.50	0.55	0.52	0.73	0.55	0.60	0.34

^aUSFWS AMNWR unpublished data

Table 2.3 Comparison of Least Auklet chick growth data (logistic model) from Kiska in 2003, St. Lawrence and the Pribilof Islands.

<i>Island</i>	<i>Asymptotic mass (g)</i>	<i>Adult mass (g)</i>	<i>Fledging mass (g)</i>	K^a	$K(a)/4^b$	<i>Source</i>
St. Lawrence	86.5	92	81 (88) ^c	0.244	5.28	Sealy (1968, 1973)
St. Lawrence	90.8	82-87	82 (100)	0.216 ^d	4.9	Piatt <i>et al.</i> 1990a
Pribilof Islands	95.8	84.4	91.5 (108)	0.239	5.72 ^d	Roby and Brink 1986
Kiska	67.9	81.5	73.2 (90)	0.150 ^e	2.55 ^e	This study (2003)

^aMean instantaneous growth rate calculated from individual chicks fit to logistical model

^bMaximum instantaneous growth rate, where a = asymptotic mass (Hussell 1972, Sealy 1973)

^cFledging mass (% adult mass)

^dEstimated using data in this table

^eBootstrap estimate

Table 2.4 Comparison of Least Auklet chick growth data from Kiska and Kasatochi Islands in 2002 and 2003.

	Kiska				Kasatochi ^a							
	2002 (n=5)		2003 (n=23)		2002 (n=10)		2003 (n=14)					
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range			
Mass (g/day)	1.1	1.0	-0.2 – 2.2	3.0	1.0	1.4 – 4.8	4.4	0.7	3.6 – 5.4	4.1	1.7	-1.5 – 5.8
Wing Chord (mm/day)	1.9	1.1	0.0 – 2.9	2.7	0.8	0.5 – 4.4	3.8	0.6	3.0 – 5.1	2.7	1.1	0.5 – 1.3

^aUSFWS AMNWR unpublished data

Table 2.5 Summary of the ten best models of Least Auklet survival at Buldir (Jones *et al.* 2002), Kiska, Kasatochi (Barton and Lindquist 2003) Islands during 1990 – 2003 (c-hat adjusted to 1.98)

<i>Model</i>	<i>QAICc</i>	<i>Delta QAICc</i>	<i>QAICc Weight</i>	<i>Number of Parameters</i>	<i>Deviance</i>
$\phi(\text{Random effects island} \cdot \text{year})$	2534.13	0	0.99963	25	596.64
$\phi(\text{island} \cdot \text{year})$	2550.41	16.28	0.00029	38	587.08
$\phi(\text{island})$	2554.98	20.85	0.00003	24	620.18
$\phi(\text{year})$	2555.42	21.29	0.00002	33	602.30
$\phi(\text{island} \cdot \text{year})$	2556.26	22.13	0.00002	33	603.14
$\phi(\cdot)$	2557.77	23.64	0.00001	22	627.02
$\phi((a1, a2 \cdot \text{year}) \cdot \text{island})$	2560.78	26.65	0	42	589.25
$\phi(\text{island})$	2566.83	32.70	0	6	668.36
$\phi(\text{island})$	2567.65	33.52	0	16	649.04
$\phi(\text{island} \cdot \text{year})$	2568.52	34.39	0	25	631.68

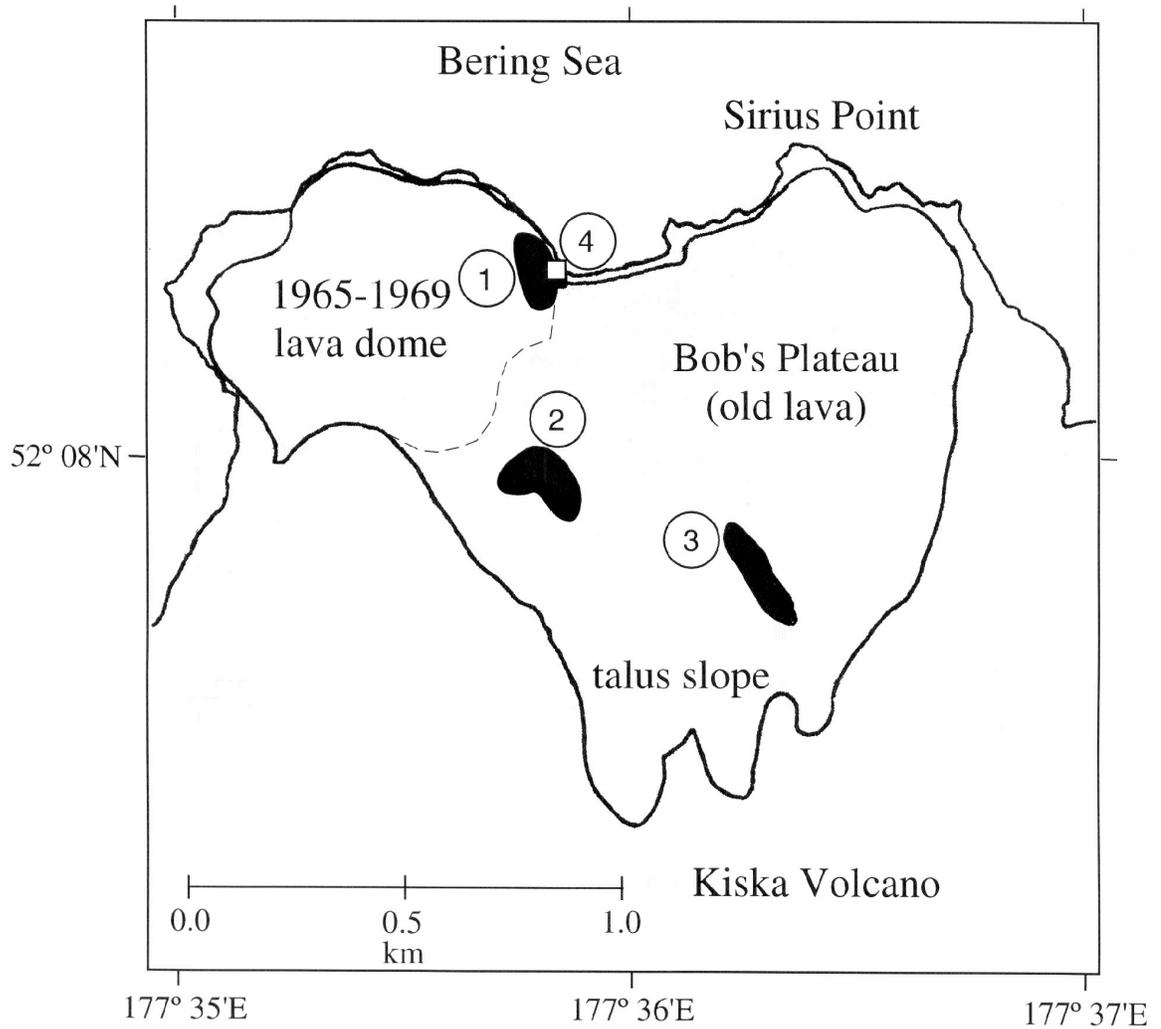


Figure 2.1 Map of Sirius Point showing the Least Auklet colony boundaries and the locations of the three productivity monitoring plots (1 – new lava, 2 – old lava low, and 3 – old lava high) and the banding plot (4).

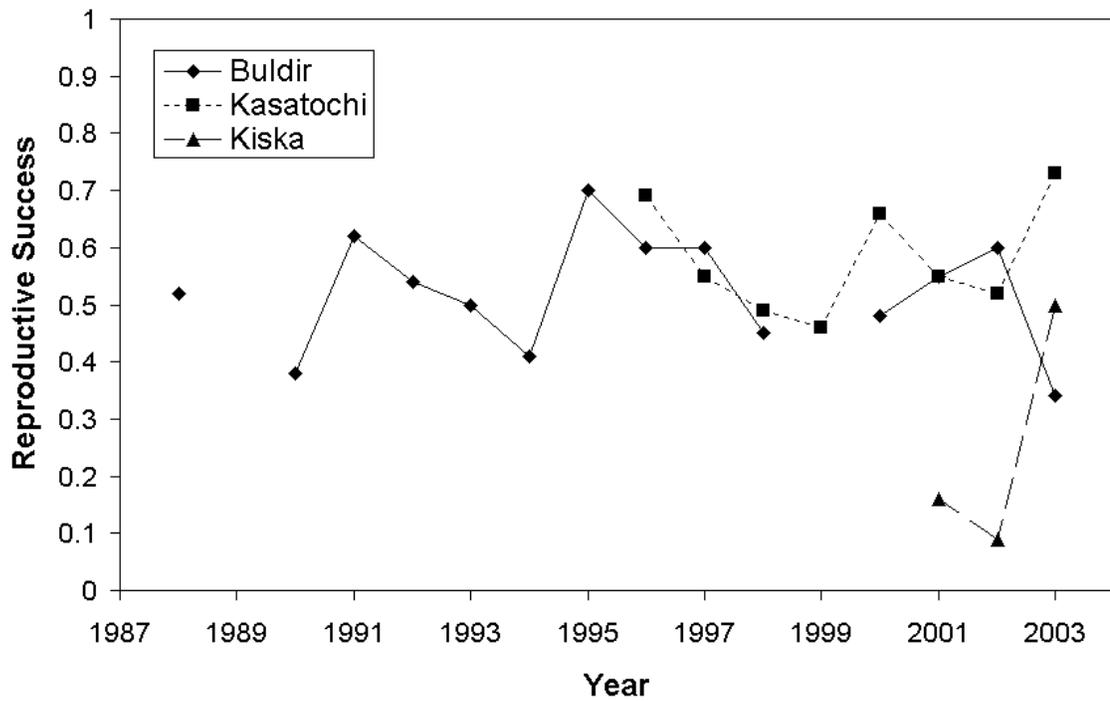


Figure 2.2 Comparison of the annual estimates of Least Auklet reproductive success at Buldir (USFWS AMNWR unpubl. data), Kasatochi (USFWS AMNWR unpubl. data) and Kiska Islands during 1988 – 2003.

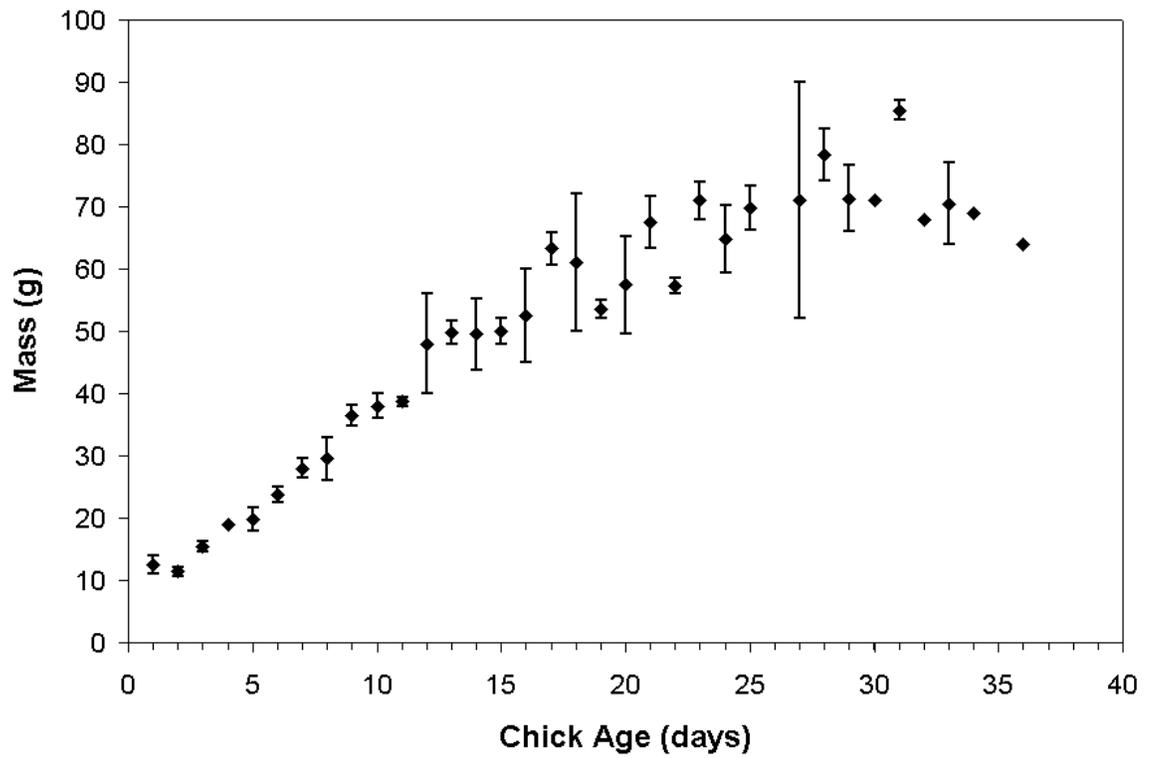


Figure 2.3 Summary of the age specific body mass of Least Auklet nestlings at the Sirius Point auklet colony in 2003 (means \pm SE).

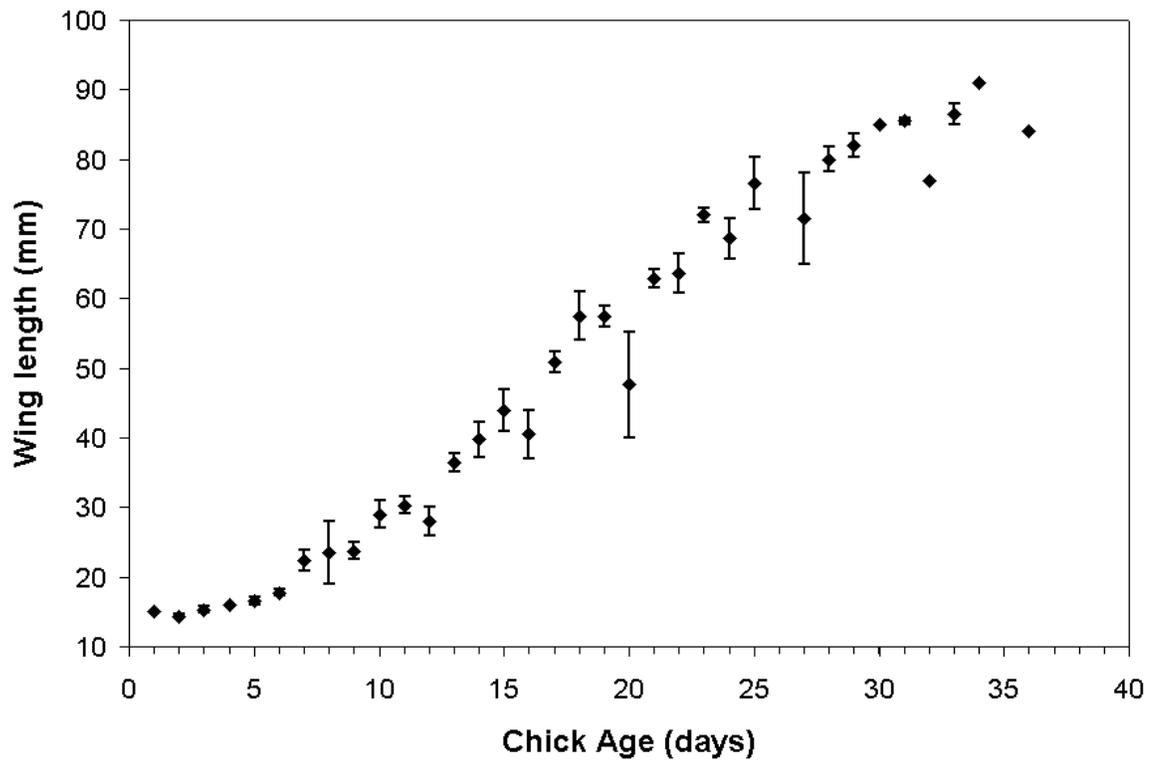


Figure 2.4 Summary of the age specific wing chord length of Least Auklet nestlings at the Sirius Point Auklet colony in 2003 (means \pm SE).

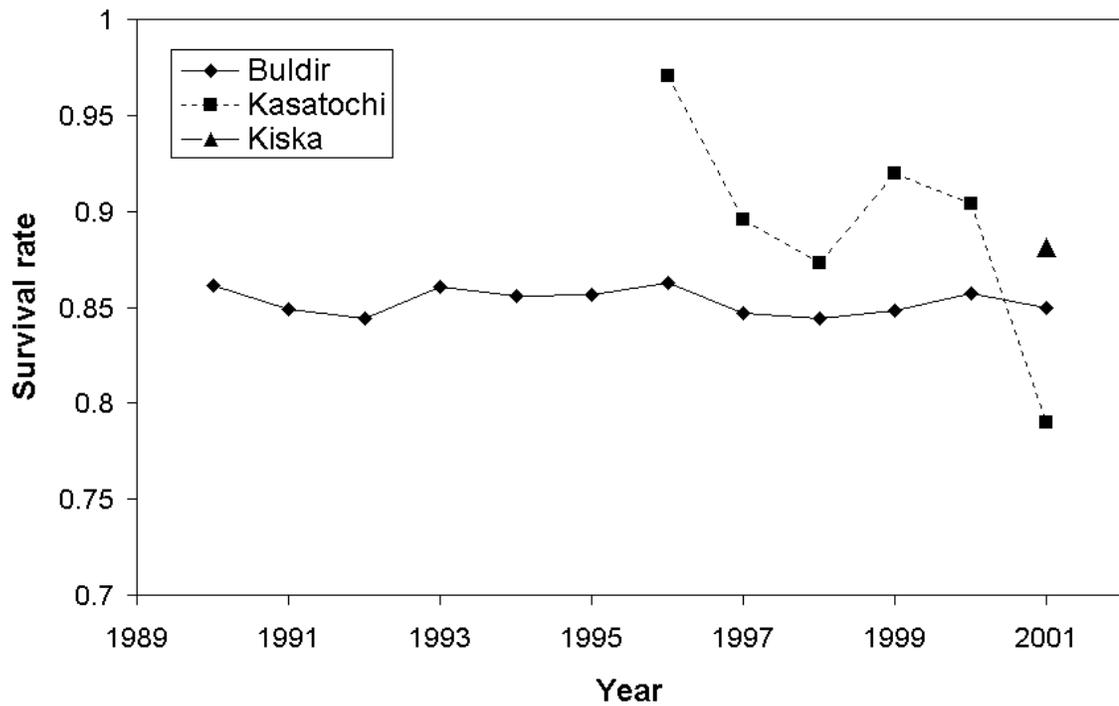


Figure 2.5 Comparison of the annual survival estimates from Buldir (USFWS AMNWR unpubl. data), Kasatochi (USFWS AMNWR unpubl. data) and Kiska Islands during 1990 – 2001, estimated from the most parsimonious model ($\phi((\text{Random effects island}) \cdot \text{year})$ $p(\text{island} \cdot \text{year})$).

CHAPTER THREE

UNNATURAL SELECTION? PREDATION ON LEAST AUKLETS (*AETHIA PUSILLA*) BY INTRODUCED NORWAY RATS (*RATTUS NORVEGICUS*) AT KISKA ISLAND, ALEUTIAN ISLANDS, ALASKA

ABSTRACT

Declining numbers of breeding seabirds have been attributed to introductions of Norway rats (*Rattus norvegicus*) onto oceanic islands around the world. The objectives of this study were to elucidate the abundance, distribution and feeding ecology of introduced Norway rats on Kiska Island, Aleutian Islands, Alaska during 2001 – 2003 in relation to seabird conservation. Rat distribution was assessed by surveying accessible parts of Kiska Island on foot to look for sign, snap-trapping rats to quantify their size, mass, and breeding status and searching for and identifying the contents of food hoards to quantify Norway rat prey selection. Norway rat sign was abundant at Kiska in areas with access to breeding seabirds and marine sources of food (intertidal areas). At the Sirius Point auklet colony (where rats have access to the intertidal zone and to breeding auklets) there was a larger proportion of juveniles to adult rats (0.58 Sirius Point versus 0.30 Christine Lake) and a larger mean adult body size (257 g and 37 cm Sirius Point versus 236 g and 35 cm Christine Lake) than at Christine Lake (10 km from the auklet colony). Surplus killing and food hoarding by rats was noted in the first week of June (early in the auklet breeding season) in all years at Sirius Point and all auklets taken were adult breeders (8 – 148 individuals per hoard, n = 7). Most rat predated auklets were taken while incubating.

The presence of Fork-tailed Storm-Petrels ($n = 7$) in one hoard indicates the persistence of this species at Kiska Island. Frequency of rat sign varied from year to year at Sirius Point. Further studies are required to directly measure the diet and importance of Least Auklets in the diet around the Sirius Point auklet colony and to assess the distribution, abundance and diet of Norway rats in inland areas on Kiska Island.

3.1 INTRODUCTION

Extinctions of insular avifaunas as the result of human predation, disturbance and accidental and deliberate introduction of non-indigenous species (NIS), especially rats (*Rattus*), have been occurring since human occupation of islands began over 30 000 years ago (Steadman 1995, 1999, Steadman *et al.* 2002). Since 1600, 93% of the 93 species and 83 subspecies of birds that have gone extinct have been insular forms (King 1985). The main cause of these extinctions was predation by NIS. Seventy percent of the extinctions of island birds have been attributed to predation, and of these 54% have been attributed to rats (King 1980). Non-indigenous rat species are now present on more than 80% of major islands (Shrader-Frechette 2001) and are major predators of seabirds (Moors and Atkinson 1984, Atkinson 1985). Three species of *Rattus* (*rattus*, *exulans* and *norvegicus*) are known to have caused declines (e.g., Harris 1970, Bertram 1995, Key *et al.* 1998, and McChesney and Tershy 1998) or extirpations (Atkinson 1985) of insular avifaunas. The black rat (*R. rattus*) has been implicated most frequently in the declines of insular bird populations; however, the Norway rat (*R. norvegicus*) has also been implicated (Atkinson 1985).

Austin (1948) emotively described the Norway rat as “a wanton wasteful predator”. Norway rats are an omnivorous, generalist predator known to prey on nesting birds (including adults, eggs and nestlings) and intertidal invertebrates (Landry 1970, Moors 1990, Drever and Harestad 1998). When compared with two other *Rattus* species, the Norway rat has the largest impact on burrow and surface nesting seabirds (Moors and Atkinson 1984), possibly because of their large size (Imber 1975). Birds are at most risk

from a predator with a body weight equal to or larger than their own, so effects of rats have been most severe (although not limited to) on smaller seabird species such as storm-petrels (Hydrobatidae) and small alcids (e.g. murrelets; Bertram 1995).

Surplus (the killing of prey without consumption) or excessive (the killing of more prey than can be consumed) killing (Kruuk 1972, Carbyn 1983) and food caching, or hoarding, has been described by Okansen *et al.* (1985) as a hunting strategy for small generalist predators like the Norway rat. These authors suggest that even partial consumption of a hoard can increase a predator's fitness. So surplus or excessive killing could be adaptive for predators that live in cold or dry environments, where hoards of prey items would not decay quickly. Norway rats hoard food (Bindra 1948a, b, Licklider and Licklider 1950, Takahashi and Lore 1980), which may be related to level of food deprivation or starvation (Fantino and Cabanac 1980, Cabanac 1985 and Cabanac and Swiergiel 1989).

Norway rats were introduced to Kiska Island (Aleutian Islands, Alaska) during or just after the Second World War (Murie 1959). They were noted as a predator on Least Auklets (*Aethia pusilla*) at the Sirius Point auklet colony in 1996 by Alaska Maritime National Wildlife Refuge (AMNWR) biologists. The Sirius Point auklet colony is likely the largest auklet colony in Alaska and has experienced almost complete reproductive failure in 2001 and 2002, possibly due to predation by Norway rats. The Least Auklet are the smallest of the alcids, having a mean adult body mass of 85 g, less than 50% of mean body mass of an adult Norway rat (Roby and Brink 1986, Jones 1993a). Least Auklets may be particularly vulnerable to predation by the Norway rats because they nest on

remote islands in large colonies in small rock crevices (Bédard 1969a, Knudston and Byrd 1982).

The purposes of this study were to describe age, sex and size structure and distribution of Norway rats on Kiska Island, describe their predation on Least Auklets and evaluate the impact of predation on Least Auklet breeding and recruitment. It was hypothesized that Least Auklets are the main prey of Norway rats, and that because rats will be able to subsidize their diet with auklets at Sirius Point they will be larger and more abundant in and around the auklet colony than elsewhere on the island.

3.2 METHODS

3.2.1 Study Area

This research was undertaken at Kiska Island (52°N 177°E), the second largest island in the Rat Islands group in the western Aleutian Islands, Alaska. Kiska is 39.8 km long and varies in width from 2.8 km to 11 km, with a total area of 28,177 ha. Kiska Volcano (1232 m elevation) is the western-most active volcano in the Aleutian Island chain and dominates the northern tip of the island. At Sirius Point (52°08'N 177°37'E) a large Least and Crested (*Aethia cristatella*) Auklet colony is situated on two lava domes located at the base of the northern slope of the volcano. The most recent of these formed during January 1962 – September 1969, the last major eruption of the volcano (Miller *et al.* 1998). The auklet colony is 1.8 km² in area and includes approximately 3 – 6 million

Least Auklets (I. L. Jones unpubl. data). This colony, located on the Alaska Maritime National Wildlife Refuge (AMNWR) is likely the largest auklet colony in Alaska.

3.2.2 Distribution

The distribution of Norway rats was assessed by utilizing Norway rat sign and limited snap trapping as evidence of rat presence or absence, rather than density, for various locations because I was unable to identify a suitable quantitative trap line sampling protocol applicable to all parts of Kiska Island. Nevertheless, I estimated abundance of Norway rat sign using three categories. During repeated ground foot surveys rat sign abundance was noted as absent (where there was no sign found), low (where rat sign was found occasionally but was not prominent) or high (where rat sign was prominent). I estimated presence / absence rather than density because routinely operated rat trap lines (e.g., Stapp 2002) in and around the auklet colony would have resulted in unacceptable mortality of auklets, which were rapidly disturbed and killed or injured by snap traps set anywhere near occupied breeding site crevices at the colony. Rat sign abundance and biology could not be rigorously assessed at inland locations on Kiska Island, because these areas were mostly inaccessible to me. Furthermore, snap traps baited with peanut butter, apple, auklet flesh and other food items were ignored by rats at the colony site, presumably because of the abundance of fresh food (auklet adults, nestlings and eggs). I was unable to identify a bait that Norway rats at the Sirius Point auklet colony would take and auklet-proof rat traps in wooden boxes failed to catch rats when used by AMNWR biologists in an earlier study at Kiska. The most successful

method for trapping rats at the colony site was to set unbaited traps along obvious worn rat trails in a few areas with tall grass. Nevertheless, using the simple detection method and by assessing detections by habitat types (coastal, colony, plateaus without access to the intertidal, etc.) I believe that I have formed a useful picture of rat distribution around the Sirius Point auklet colony, Kiska volcano and the Lake District.

The spring and summer distribution of rats on parts of Kiska Island was assessed by noting the location, presence / absence and type of sign [feces, trails, diggings, and prey remains (of eggs, adults, and nestling auklets)] when present while hiking from sea level to the top of the volcano, and including the northwest side of Kiska Island from Sirius Point to Witchcraft Point ($52^{\circ}03.077'N$ $177^{\circ}30.608'E$); the shores of Christine, East and West Kiska Lakes; beaches in Kiska Harbor; meadows around North Head and nearby Salmon and Trout Lagoons; and meadows plus subalpine areas between Kiska Harbor and Conquer Point, including the large west-facing beach below this point ($51^{\circ}59.313'N$ $177^{\circ}29.477'E$; Figure 3.1). To indicate the presence or absence of rats outside the auklet colony traplines were used in addition to rat sign. Traplines were set in transects and traps were spaced approximately 10 m apart. During 19 – 26 June 2002 a trapline (30 snap traps baited with peanut butter) was set on a subalpine *Calamagrostis* meadow at 60 m asl between the west side of Sirius Point and Wolf Point ($52^{\circ}07.591'N$ $177^{\circ}35.124'E$). This trapline was checked once every 24 hours and subsequently relocated to a grassy covered lava flow at 90 m asl ($52^{\circ}07.531'N$ $177^{\circ}35.096'E$) for the period 26 June – 25 July. This information was used to map rat abundance and distribution on the northern part of Kiska Island. The rat presence / absence data were

assessed from the three years of the study to detect annual variation in the distribution of rats both on and off the Sirius Point auklet colony.

3.2.3 Norway rat Population Structure

Rats were caught using snap traps set along rat trails at the auklet colony and along the beach berm at Christine Lake (a large brackish water lake located seven kilometers south of the auklet colony, 52°04.986'N 177°33.100'E) in late May – early June and late July – early August in 2002 and 2003. The snap traps were set unbaited at the colony site in obvious worn rat trails in dense grass. At Christine Lake the traps were baited with fresh Dolly Varden (*Salvelinus malma*) and placed along the beach berm and on obvious worn rat trails along the shore of Christine Lake. Dolly Varden was tested as bait at Christine Lake because it was assumed be a part of the diet of the rats at Christine Lake. During the four trapping intervals, traps were set out at night and checked early the next morning until at least 10 rats were caught (approximately 2-3 nights with 16 traps). In 2003 rats were also trapped at East Kiska Lake (an inland freshwater lake near Christine Lake; 52°04.470'N 177°35.096'E) with snap traps baited with fresh Dolly Varden (two trapping nights with 15 traps). Body mass and total length were measured on all specimens taken in both years; in 2003 tail length was also measured. Rats were also sexed and the reproductive condition of mature females (females weighing more than 150 g and longer than 32 cm) was noted (pregnant; number of embryos if pregnant; lactating). A two-way ANOVA was used to test for significant differences in mass and total length between sexes and across locations.

3.2.4 Diet Composition

Norway rat feeding ecology was not comprehensively assessed in this study and only included inferences to prey selection based on the contents of hoards found at the colony and the known diets of Norway rats in other regions. Norway rat food hoards were examined and their contents noted to infer diet at Sirius Point.

3.2.5. Prey Selection

Using Grant's (1972) methods (using t-tests to find the differences between means and variances) I assessed whether the birds killed by rats and found in rat food hoards at Sirius Point differed significantly in wing length, knob size or plumage class from those captured at the banding plot (birds believed to be representative of all Least Auklets breeding at the Sirius Point auklet colony; Jones *et al.* 2002). A significant difference in either the means or variances of the birds killed by rats would suggest that rats are exerting a natural selective force on the Least Auklets breeding at the Sirius Point colony (Endler 1986).

Food hoards were searched for throughout the auklet breeding seasons in 2002 and 2003. Contents of hoards were identified and counted, and the condition (whether the item was fresh, slightly decayed or in the late stages of decay) of each item was noted. Measurements of wing chord to the nearest 1 mm using a wing rule, and bill knob (an ornament that is located on the upper part of the bill) to the nearest 0.1 mm using dial calipers from each auklet found in the food hoards was taken. Auklets were sexed by dissection unless they were badly decomposed, and plumage class was noted (0 – white,

1 – lightly flecked, 2- moderately flecked, or 3 - heavily flecked; Jones 1990). These data were compared with similar measurements from a sample of live birds captured randomly for banding using noose carpets at one banding study plot on Kiska Island. Preliminary analysis of variance comparing the knob size of auklets caught randomly on the banding plot revealed that those birds measured early in the breeding season (prior to the mean hatching date) had a significantly larger (p-value = 0.0001) mean knob size than those measured randomly on the banding plot after the mean hatching date. Since all birds from the hoards were measured in early June (prior to the mean hatching date) only those birds measured randomly on the banding plot prior to the mean hatching date were used (14 June – 27 June 2001, 08 June – 06 July 2002).

3.3 RESULTS

3.3.1 Distribution

Norway rat sign was most abundant in all areas with accessible intertidal zones (i.e., everywhere except below steep sea cliffs) and in coastal areas at the Sirius Point auklet colony on Kiska in all years (2001 – 2003; Figure 3.1, Appendix B). Numerous rat tracks were observed near and above the high water mark on all sandy sea beaches visited throughout the study. Norway rat sign, including evidence of digging and fresh scat, was also plentiful along the entire shoreline of Christine Lake and along the shoreline of West Kiska Lake, within 500 m of the ocean. Rat sign was most abundant at the auklet colony site, and evidence of over-winter occupation (abundant weathered droppings found in late May) was present in areas with access to intertidal boulder

beaches. Norway rat sign was rare on plateaus and inland meadows, and no sign was found above 200 m asl. In all years, evidence of rats over-wintering (tunnels in grass and earth burrows) on a steep hillside with dense grasses and herbs 200 m south of the colony site at 52°07.784'N 177°35.396'E was observed. Trapping success at inland meadows between Sirius Point and Wolf Point was zero (1080 trapping nights). The most inland (from the ocean) detection was of two adult male rats trapped at the north end of East Kiska Lake (an inland freshwater lake) in June 2003 (30 trapping nights). Between years at Sirius Point, anecdotal evidence (abundance of rat sign and ease of rat capture in snap traps) suggests that Norway rat abundance was most variable early in the auklet breeding season. Early season Norway rat sign around the colony was observed to have been highest in 2002 and lowest in 2003. However, in all years Norway rat sign was abundant and did not seem to differ by the middle of the auklet breeding season. Around camp Norway rat sign was not abundant, however in 2003 rats entered the camp food supply for the first time.

3.3.2 Norway rat Population Structure

Significantly more juvenile rats were caught at Sirius Point (0.61) than at Christine Lake (0.30; $\chi^2 = 11.285$, $df = 1$, p -value = 0.001). At Sirius Point the sex ratio was significantly biased towards males ($\chi^2 = 5.333$, $df = 1$, p -value = 0.021) and was approximately 2:1, but at Christine Lake the sex ratio was not significantly biased ($\chi^2 = 0.800$, $df = 1$, p -value = 0.371) and was approximately 0.8:1. However, there were no significant differences detected in the sex ratios between the two locations ($\chi^2 = 2.828$, df

= 1, p-value = 0.093). The proportion of adult females with obvious signs of reproductive status did not differ significantly between Sirius Point and Christine Lake (0.50:0.27; $\chi^2 = 1.364$, df = 1, p-value = 0.243).

Measurements of Norway rats are summarized in Table 3.1 and Figure 3.2. No significant differences were detected between the sexes for mass and length [p-value = 0.946 (mass) and 0.712 (length)] or between the interaction term (sex*location) [p-value = 0.875 (mass) and 0.781 (length)]. Rats caught at Sirius Point were significantly larger in total length than those caught at Christine Lake (p-value = 0.033), but there was no significant difference in the mass of the rats caught (p-value = 0.240) between the two locations (Sirius Point and Christine Lake).

3.3.3 Diet Composition

Food hoarding by Norway rats on Kiska Island was observed in all three years of this study. Hoards of cached auklets were found early in the breeding season on Kiska and included hoards in excess of 100 freshly killed adult Least Auklets. Those found later in the breeding season contained eggs (usually addled) and adult Least Auklets in late stages of decomposition with little evidence of consumption. No hoards of fresh birds were found after early June. Under the assumption that Norway rats hoard their main prey, the principal prey of the rats in the vicinity of Sirius Point in 2001 – 2003 was adult Least Auklets. There were no hoards found that contained Least Auklet sub-adults or nestlings. Each year I found a few Crested Auklets that had obviously been predated

by rats, but none were found in hoards. Six adult Fork-tailed Storm-Petrels (*Oceanodroma furcata*) were found in one large hoard in 2002.

3.3.4 Prey Selection

All Least Auklets in hoards were found early in the auklet breeding season and in adult plumage. There was no sex bias detected in the hoarded birds nor were significant differences found for the mean wing chord length, knob size or plumage class in auklets found in the hoards compared to those captured randomly on the banding plot (Table 3.2). Additionally, there were no differences between the variances of the traits for wing chord length and plumage class. However, knob size had a significantly smaller variance in the hoarded birds than those captured randomly on the banding plot (Table 3.3).

3.4 DISCUSSION

Introduced Norway rats have been altering the ecosystem of Kiska Island since their introduction during the Second World War. The species is omnivorous and a generalist predator that feeds on the most abundant and highest nutritional value food available (Drever and Harestad 1998). Norway rats are known predators of burrow- and crevice-nesting birds and have been implicated in the declines and extirpations of some species of seabirds (Moors 1990, Drever and Harestad 1998, Atkinson 1985). The goal of this study was to elucidate the distribution, population structure and feeding biology of Norway rats on Kiska Island in order to better understand this introduced species and what impacts it might be having on the large auklet colony at Sirius Point.

Many studies have addressed the impacts of introduced Norway rats on island ecosystems, including Langara Island, Queen Charlotte Islands, Canada (Bertram and Nagorsen 1995) and Sasudo Island, Korea (Lee and Yoo 2002). These studies focused on impacts on insular avifauna and provide little information concerning the general biology of the rats themselves. On the Shiant Islands, Scotland, Black rats were more abundant and larger where they can subsidize their diet with marine sources of food (Stapp 2002, MacLennan *et al.* 2000, and Key *et al.* 1998). Similarly, if rats occur in any area (i.e. intertidal zone or seabird colony) with an extreme abundance of prey, they could subsidize their diet and would be more abundant and reach larger sizes than those feeding in areas away from this extreme abundance of prey. At the Sirius Point auklet colony on Kiska Island, Norway rats have relatively easy access to an extreme abundance of avian prey (Least Auklets). Similar to Black rats on the Shiant Islands (Stapp 2002), Norway rats are larger in size and have increased reproductive activity where the rats can subsidize their diet with auklets on Kiska Island (i.e. Sirius Point).

Hoarding behaviour in rats has been shown to be regulated by food deprivation and starvation (Fantino and Cabanac 1980, Cabanac 1985, Cabanac and Swiergiel 1989). Knowing this it has been hypothesized that at Kiska, Norway rats begin hoarding when the auklets arrive at the colony and this behaviour then becomes less frequent and likely ceases by the middle of the incubation period when rats would no longer experience food deprivation. This hypothesis cannot be rejected and is supported by the absence of sub-adults and nestlings from the rat hoards and the hoards found after early June containing adult Least Auklets in late stages of decomposition. In addition to adult Least Auklets

found in the food hoards, Fork-tailed Storm-Petrels were found in one hoard in 2002. This species is not known to breed at Kiska even though there is suitable habitat available and birds were occasionally heard vocalizing at night near camp. They do however breed in the Aleutian Islands and are an abundant breeder on Buldir Island (approximately 119 km west of Sirius Point). The presence of this species in the food hoard suggests their persistence at Kiska.

Surplus killing and food hoarding of adult Least Auklets by Norway rats early in the auklet breeding season may be having a significant impact on the Least Auklet breeding population on Kiska Island, especially in years following mild winters and when early spring rat abundance is likely high. Piatt *et al.* (1990b) and Jones (1992a) showed that breeding adult auklets arrive at the colony first and establish their breeding territories; sub-adults arrive 2-3 weeks later after egg laying has occurred. The age / experience hypothesis suggests the earliest birds to arrive at breeding colonies are those that are older and more experienced (Hedgren 1980). This hypothesis has been supported for many species of birds including alcids [e.g. Thick-billed Murres, *Uria lomvia* (DeForest and Gaston 1996)]. At the Sirius Point auklet colony those birds found hoarded by Norway rats early in the season would thus be those individuals most experienced and most likely to fledge a chick. These experienced breeders would be expected to have more pronounced ornaments than sub-adults and non-breeding individuals.

Jones and Montgomerie (1992) found that Least Auklet ornamental traits were weak predictors of condition, and that the bill ornament (knob) was larger in non-

breeding birds. They add that this is opposite of the prediction that ornaments should be more pronounced in breeding birds. However, in a monomorphic species with high mate fidelity, it is possible that birds advertising their reproductive status (birds that are not already paired) may keep their ornaments large even after breeding has begun to attract a mate. While those that are already paired would not be required to further advertise their status. An example is the rictal plate (a bright orange bill plate) of the Crested Auklet (*Aethia cristatella*) which is only present in breeding birds until the chicks begin to hatch, but lasts longer in non-breeding birds (H. L. Major pers. obs.). This also appears to be the case for knob size in Least Auklets, where birds measured prior to the mean hatching date had a larger mean knob size than those measured after the mean hatching date. Least Auklets found hoarded by rats did not differ significantly from those measured on the banding plot prior to hatching, but those found in the hoards had a smaller variance around their knob size. The smaller variance around the knob may be the result of young birds (sub-adult birds being confused as adult birds) with very small knobs being included in the randomly sampled individuals from the banding plot. These data support the hypothesis that the birds found in the rat hoards are a random sample of the adult Least Auklet population prior to hatching.

As in a study of Black rats on the Shiant Islands (Stapp 2002), Norway rats at Kiska tended to be larger in size and had a larger proportion of juveniles to adults in the population in areas of increased food availability. In addition, the surplus killing and food hoarding behaviour of Norway rats on Kiska Island may be having a selectional force for the earliest auklets to arrive at the colony, or the adult experienced breeders.

This may have a drastically more negative impact than if they were hoarding a random sample of the population (breeding and non-breeding individuals). For example, if Norway rats on Kiska are killing and hoarding proportionally more experienced adult breeders than any other individuals this will not only lower adult survival but also reproductive success. Whereas, if they are hoarding a random sample of the population (adult breeders, non-breeders and sub-adults) this will also have a negative impact on survival but will not have as great an impact on reproductive success.

To fully understand the impacts of the Norway rat on Kiska Island more studies need to be carried out to elucidate the biology and abundance of inland rats, how and why the rat population varies from year to year, differences in the feeding ecology between the colony, coastal and inland areas, and the timing and selective forces associated with timing of hoarding by the Norway rats. In addition too further studies of impacts of rats on auklets, stable isotope studies need to be carried out to determine the importance of Least Auklets in the diets of the Norway rats and a population viability analysis should be performed to determine the sensitivity of the auklets to predation.

Table 3.1 Summary of measurements on adult Norway rats (*Rattus norvegicus*) trapped at the Sirius Point auklet colony and Christine Lake (coastal) in 2002 and 2003. Data are shown as mean \pm SE (n).

		<i>Sirius Point</i>	<i>Christine Lake</i>
Mean Mass (g)	Male	254.8 \pm 18.3 (16)	236.8 \pm 16.8 (13)
	Female	258.8 \pm 25.7 (8)	235.2 \pm 8.6 (15)
Total Length (cm)	Male	37.1 \pm 1.1 (16)	34.9 \pm 0.7 (18)
	Female	37.2 \pm 1.3 (8)	35.5 \pm 0.4 (22)

* 4 females from Sirius Point and 6 from Christine Lake were pregnant or lactating.

Table 3.2 Comparison of the mean trait sizes (wing chord, knob size and plumage class) of auklets measured randomly on the banding plot (plot) and those found killed in the rat hoards (hoard) of Least Auklets. Data are shown as mean \pm SE (n).

<i>Trait</i>	<i>Group</i>	<i>Mean</i>	<i>t</i>
Wing Chord	Hoard	98.69 \pm 0.20 (116)	-1.31
	Plot	98.21 \pm 0.30 (57)	
Knob	Hoard	1.51 \pm 0.04 (110)	-0.56
	Plot	1.46 \pm 0.08 (55)	
Plumage class	Hoard	2 \pm 0.05 (109)	-1.10
	Plot	2 \pm 0.05 (57)	

* p-value $< \alpha = 0.017$ (using Bonferroni adjustment, $\alpha = 0.05 / 3$)

Table 3.3 Comparison of the variances traits (wing chord, knob size and plumage class) of auklets measured randomly on the banding plot (plot) and those found killed in the rat hoards (hoard) of Least Auklets. Data are shown as mean \pm SE (n).

<i>Trait</i>	<i>Group</i>	<i>n</i>	<i>Variance</i>	<i>t</i>
Wing Chord	Hoard	116	1.75	0.26
	Plot	57	1.91	
Knob	Hoard	110	0.07	2.30*
	Plot	55	0.38	
Plumage	Hoard	109	0.21	-0.57
	Plot	57	0.19	

* p-value $< \alpha = 0.017$ (using Bonferroni adjustment, $\alpha = 0.05 / 3$)

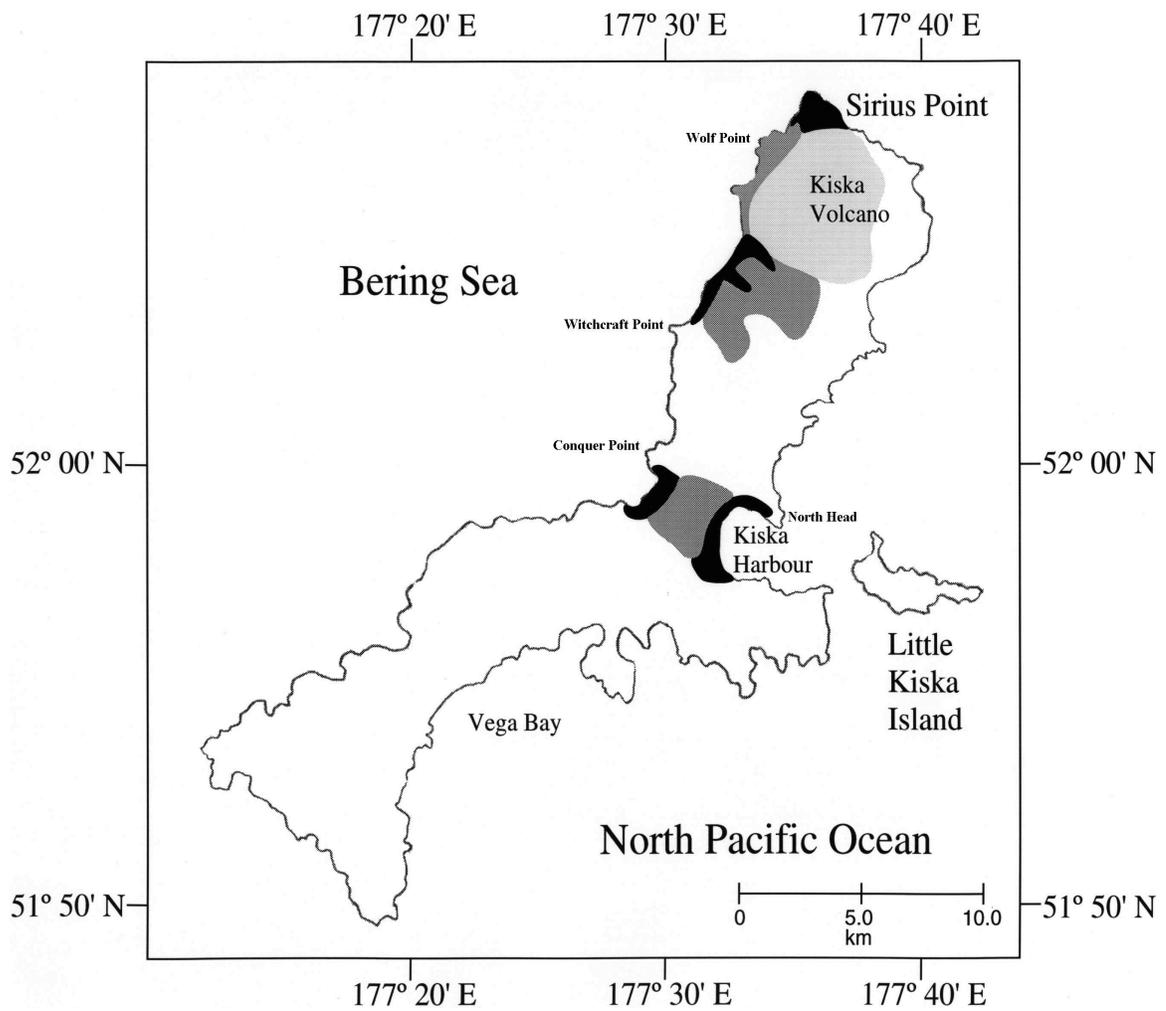


Figure 3.1 Map of Kiska Island showing rat distribution (white areas have were not visited during the study, light gray represents the absence of rats, dark gray represents low abundance of rat sign, and black represents high abundance of rat sign).

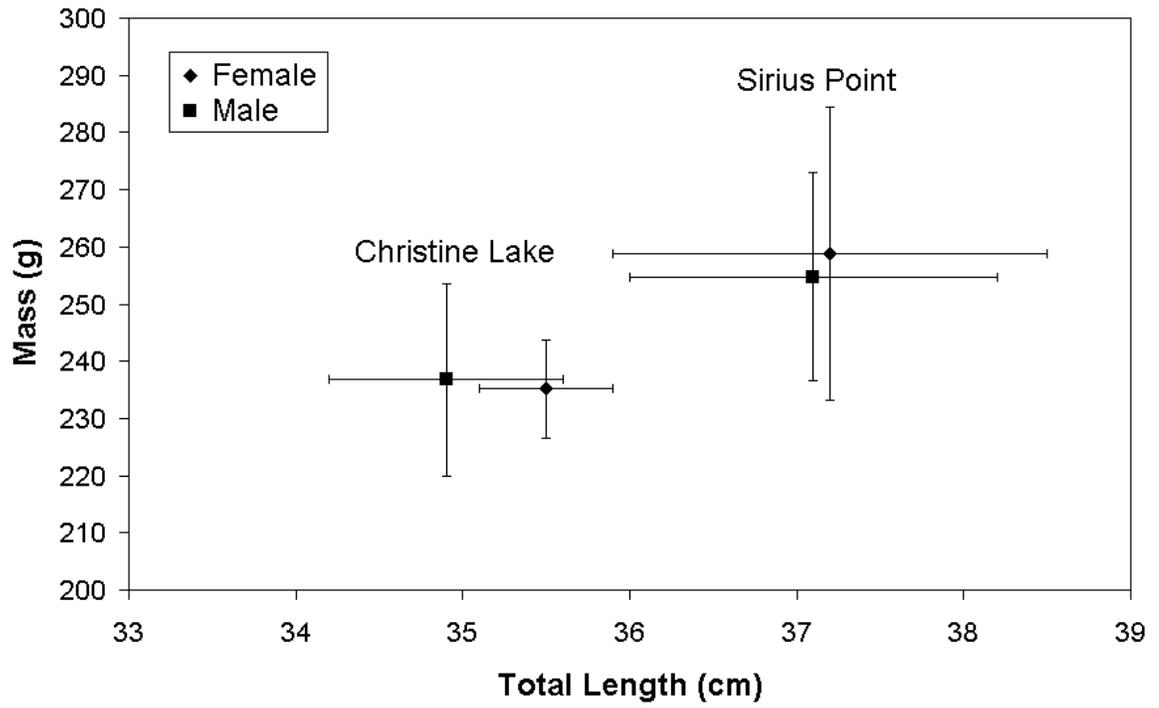


Figure 3.2 Comparison of the overall mean size (mass and total body length) of adult Norway rats caught at Sirius Point and Christine Lake in 2002 and 2003. Data are means \pm SE.

CHAPTER FOUR:
A STAGE-BASED POPULATION MODEL FOR LEAST AUKLETS
(*AETHIA PUSILLA*) BREEDING AT KISKA ISLAND UNDER TWO
MANAGEMENT SCENARIOS

ABSTRACT

Population viability analysis (PVA) is widely used as a tool for conservation biology, to assess extinction risk and forecast future population size. In particular, perturbation analysis (sensitivity and elasticity analysis) is useful to determine which life-history traits are most important to changes in population growth rate (λ). The goals of this study were to assess the potential impacts of introduced Norway rats (*Rattus norvegicus*) and various management options to preserve the Least Auklet (*Aethia pusilla*) colony at Sirius Point, Kiska Island, Alaska. Perturbation analysis was run on the best estimates of vital rates (mean vital rates) from Kiska and revealed a λ of 0.9139, a decreasing population. It also revealed that adult survival and juvenile mortality are the vital rates most important to changes in λ and thus those most important to have accurate estimates of, and for conservation. The single available estimate of adult survival at one study plot at Kiska (0.88, 2001 – 2002) was approximately average for the species, therefore management plans aimed at increasing this parameter to increase λ may not be feasible. However, juvenile mortality was high, especially during the first week after hatching at replicated study plots throughout the colony in two different years. Actions

to decrease juvenile mortality by eradicating Norway rats may be the most feasible management plan to increase λ to a population sustaining level. Three population models were run showing what may happen to the Least Auklet population under the two management plans. Under the 'do nothing' (where current vital rate estimates for Least Auklets continue indefinitely) and 'rat eradication' (where adult survival remains similar to that measured on Buldir during 1990 – 2001) options, the population will decline by greater than 92% in the next 30 years. Under the 'rat eradication' option where juvenile mortality is decreased and rats are the sole cause of the high nestling mortality and are eradicated, this model predicts that the population will increase by approximately 43% in 30 years. I recommend that continued monitoring and assessments of both direct and indirect impacts of rats be accomplished prior to implementing any management plans because of the large amount of uncertainty in the parameters used to construct this population model. However, given the current best estimate of the vital rates and the resulting rapid population decline implementing partial control measures to test productivity in 'rat-free' plots as compared to control plots will assist in determining the impacts of rats on juvenile mortality.

4.1 INTRODUCTION

Oceanic islands, islands that have never had connections with a continental landmass (Carlquist 1965, 1974, Paulay 1994), are typically highly susceptible to non-indigenous species (NIS; Moors and Atkinson 1984, Atkinson 1985). Specifically, seabirds are particularly susceptible to introductions of NIS and have experienced population declines [(e.g. the Dark-rumped Petrel (*Pterodroma phaepygia*) in Hawaii and the Galapagos; Harris 1970, Coulter 1984, Harrison *et al.* 1984] and extinctions [e.g. Guadalupe Storm-Petrels (*Oceanodroma macrodactyla*); Jehl and Everett 1985, McChesney and Tershy 1998]. Managing or mitigating the negative impacts acting on small and endangered populations as a result of NIS has emerged as a top priority in conservation biology. Population viability analysis (PVA; Boyce 1992) is one method that can be used to assess not only the viability of a small population, but also the effects of different management options (e.g. Hamilton and Moller 1995, Towns *et al.* 2003).

Population viability analysis is any analysis that uses demographic data to predict the future fate of a population (Boyce 1992, Marmontel *et al.* 1996, Coulson *et al.* 2001, Caswell 2001). PVAs are generally used to assess the probability of extinction of a small, endangered population under different management scenarios (e.g. Crouse *et al.* 1987, Doak *et al.* 1994, Reed *et al.* 1998, Akçakaya 2000, Horino and Miura 2000, Pergrams *et al.* 2000, Pfab and Witkowski 2000, Mathews and Macdonald 2001, Chaloupka 2002, Li and Jiang 2002). However, PVAs are only as reliable as the data used to construct them and when the distributions of the population growth rate (λ) and vital rates will not change with time (Doak *et al.* 1994, Coulson *et al.* 2001). Similarly,

some studies have questioned the accuracy of PVAs and shown that there is typically a considerable amount of uncertainty in estimating extinction risk (Taylor 1995, Ludwig 1999, Coulson *et al.* 2001, Lindenmayer *et al.* 2003). In light of this, many studies suggest using PVAs for guidance to the efficiencies of different management options and to address directions for further study (Possingham *et al.* 1993, Hamilton and Moller 1995, Ellner *et al.* 2002, Lindenmayer and Lacy 2002).

Perturbation analysis in PVAs is a popular analysis used to determine which population parameters, or vital rates are most important to the asymptotic properties of the population (i.e. λ ; van Groenendael *et al.* 1988). Two methods of accomplishing perturbation analysis are sensitivity analysis, the analysis of how sensitive one variable is to changes in another and elasticity analysis, or the proportional change of one variable to λ (de Kroon *et al.* 1986; McDonald and Caswell 1993, Morris and Doak 2002). These analyses give insight into which vital rates require further study and which management plans will best address those vital rates most important for conservation (e.g. Crouse *et al.* 1987, Doak *et al.* 1994, Reed *et al.* 1998, Kelly and Durant 2000, Plissner and Haig 2000).

The Least Auklet (*Aethia pusilla*) is a small, socially monogamous seabird that breeds in large colonies in small rock crevices on the Aleutian Islands and other remote islands in the Bering Sea (Bédard 1969a, Knudtson and Byrd 1982, Jones 1993a). They have relatively high adult survival (approximately 87%), a clutch size of one and an average reproductive success of 0.5 – 0.7 (Knudtson and Byrd 1982, Roby and Brink 1986, Piatt *et al.* 1990a, Gaston and Jones 1998, Jones *et al.* 2002). Least Auklets are

one of the most abundant seabirds in North America, with a conservative population estimate of 9 million (Jones 1993a). The Least Auklet colony at Sirius Point (52°08'N 177°37'E), Kiska Island, Aleutian Islands, Alaska is likely the largest auklet colony in Alaska and has been estimated at 3 – 6 million (I. L. Jones pers. comm.).

Norway rats (*Rattus norvegicus*) were introduced accidentally onto Kiska Island during the Second World War (Murie 1959). They are a known predator of crevice and ground nesting seabirds (Moors and Atkinson 1984), have been named responsible for the disappearance of some seabirds from islands (see Atkinson 1985) and have reduced the number of breeding seabirds on other islands (e.g., Ancient Murrelets *Synthliboramphus antiquus* colonies on Langara Island, British Columbia, Bertram 1995, Bertram and Nagorsen 1995). Norway rats were noticed as a predator of Least Auklets at Sirius Point by Alaska Maritime National Wildlife Refuge (AMNWR) biologists in 1996 (AMNWR unpubl. report). Concern about the impacts of Norway rats were raised when increased rat sign was noticed by AMNWR biologists around Sirius Point, Kiska Island, after the removal of introduced Arctic foxes (*Alopex lagopus*).

The goals of this study were to assess the potential impacts of the introduced rats and various management options to maintain the Least Auklet colony at Sirius Point. According to Heppell *et al.* (2000) elasticity analysis can be used to make preliminary management proposals that account for life history characteristics for data-poor populations, such as the Least Auklet population at Sirius Point, and as a first step towards modeling efforts. Accordingly, I aimed to evaluate the elasticities of Least Auklet vital rates to better understand where future research should be focused and

evaluate two management options (1) do nothing or (2) control / eradicate rats, with preliminary population models.

4.2 METHODS

4.2.1 Least Auklet Demography

Least Auklet reproductive success and survival were measured during 2001 – 2003 at the Sirius Point auklet colony, Kiska Island, Alaska. Reproductive success was assessed by monitoring ~200 active Least Auklet breeding crevices on three productivity study plots that are believed to be representative of the colony (Chapter 2, Major *et al.* ms submitted). Least Auklet breeding crevices were located, marked and monitored once every four days from late May through early August during 2001 – 2003 to assess hatching, fledging and overall reproductive success.

Least Auklets were captured for colour marking using noose carpets set on the colony surface within a single 50 m² (surface area) study plot (centered at 52°08.038'N 177°35.780'E) at Sirius Point, Kiska Island. Noose carpets were used because they are believed to randomly select breeding and non-breeding auklets from the population (Jones 1992a, b, 1993b). Each captured adult was banded with a numbered stainless steel leg band and a unique combination of three Darvik plastic colour bands. The age (other than as adults greater than two years old) and sex of each individual in the sample was unknown. Sub-adult birds (two year olds, identified by criteria described by Jones 1993b and Jones and Montgomerie 1992) were not colour banded and not included in survival analysis.

Resightings of colour marked auklets were made daily (except during bad weather conditions) during mid-May to early August (2001 – 2003), which encompassed the birds' laying, incubation and chick-rearing periods. Birds were observed attending the study plot from a plywood blind during their morning and evening activity periods (0900h – 1400h; 2200h – 0030h) and the colour band combinations of all marked individuals present were recorded. Local adult annual survival (ϕ) and recapture (p) rates were estimated (Chapter 2, Major *et al.* ms submitted) using methods described in Lebreton *et al.* (1992) and Burnham and Anderson (1998), with program MARK (White and Burnham 1999).

4.2.2 Population Viability Analysis

The main objective of this model was to assess the sensitivities and elasticities of estimated vital rates from Least Auklets breeding at the Sirius Point auklet colony on Kiska Island to better direct future research on this colony. A stage class matrix model with time series beginning at the egg stage was used as described by Lefkovitch (1965) because of the absence of demographic data for each age class. Least Auklets can breed for the first time at three years of age, the life cycle graph (Figure 4.1) was thus split into two stages, juveniles (stage 1) and adults (stage 2). Juveniles were classified as those birds two years old and younger (non-breeding birds), and adults were classified as all birds above two years old (all potential breeding birds). A stage class model, like this one, requires not only estimates for survival and fecundity but also the probability of

surviving within the stage class and the probability of remaining in one stage or moving onto the next.

4.2.2.1 Vital Rate Estimation

Monitoring of Least Auklet survival and productivity have been ongoing in long-term monitoring programs on Buldir and Kasatochi Islands in the Aleutian Islands, Alaska, by the Alaska Maritime National Wildlife Refuge (AMNWR). These data were used in addition to that collected on Kiska Island in 2001 – 2003 to determine the amount of variation within this species. Three matrices of vital rates (Table 4.1) were used in this study.

- 1) Mean vital rates as calculated from Least Auklet monitoring at Kiska Island during 2001 – 2003.
- 2) Highest and (3) lowest vital rates measured on Kiska incorporating the highest and lowest survival rates measured during long-term monitoring on Buldir and Kasatochi Islands.

Within stage survival (P_i) and the transition probability (G_i) were assessed using equations given by Crouse *et al.* (1987). Fecundity was estimated using the equation:

$$F_i = (P_i)(E_i)(M_i)$$

Where ' P_i ' is the stage specific survival probability, ' E_i ' is the proportion of stage i birds breeding and ' M_i ' is the mean fecundity at stage i . ' E_i ' was estimated from a study of Least Auklets on St. Paul Island, Alaska by Jones (1992b) and ' M_i ' was estimated to be one (Gaston and Jones 1998).

4.2.2.2 Perturbation Analysis

A MATLAB program modified to incorporate vital rates for Least Auklets from Morris and Doak (2002) was used to calculate the sensitivities and elasticities to λ for the population projection matrix using the mean (best estimate) vital rates for Kiska. I performed sensitivity analysis on both survival and mortality rates to determine if the rankings of elasticities would change (Morris and Doak 2002). In addition another MATLAB program modified to incorporate vital rates for Least Auklets from Morris and Doak (2002) was used to calculate the sensitivities from simulated random matrices between the high and low estimated vital rates. This program was used to account for uncertainty in the vital rates estimated from Kiska.

4.2.2.3 Management Options

A simple population viability analysis with no density dependence was run using a MATLAB program modified from Morris and Doak (2002) to incorporate vital rates from Least Auklets. Three population models were run, the first, the ‘do nothing’ management option, estimated what may happen to the population size if everything remains similar to that measured during 2001 – 2003. The second model ‘rat eradication 1’ was run under the assumption that rats were eradicated from Kiska and Least Auklet productivity returned to normal (0.54, the average productivity recorded at Buldir and Kasatochi Islands during 1988 – 2003; AMNWR unpubl. data). This model estimated what may happen to the population size if rats were the sole cause of the breeding failure at this colony during 2001 – 2003 and are eradicated from Kiska at the start of the time

series. The third model, 'rat eradication 2' was run under the assumption that rats are eradicated from Kiska at the beginning of the time series and Least Auklet adult survival was then similar to that measured on Buldir Island during 1990 – 2001. Simulations were run using nine population projection matrices incorporating the three current vital rate estimates from Kiska (as measured in 2001 – 2003) and the best, high and low fecundity estimates in the 'do nothing' management plan. The best, high and low estimates of productivity from Buldir and Kasatochi Islands, with the best, high and low fecundity estimates were used in the rat eradication management plan. The frequency that each matrix was used was specified, where in the do nothing option, the three matrices using the best fecundity were given higher preference (25%) over the six other matrices (4.2%). In the second model, 'rat eradication 1' the three matrices with the best productivity estimates were given higher preference (25%) over the other six (4.2%) and in the third model, 'rat eradication 2', the three matrices with the best (mean) adult survival rate were given higher preference (25%) over the other six (4.2%). This approach was used to account for some variation and uncertainty in the vital rate estimates. Five thousand simulations were run for 30 years and the mean population sizes from the simulations graphed.

The estimate for Least Auklet adult survival from Kiska in 2001 was used and held constant over all simulations in the first two management models (do nothing and rat eradication 1). This was done because it is the sole estimate available for Kiska and was not significantly different from the mean survival estimates from Buldir and Kasatochi. Additionally, Least Auklet adult survival has been shown to vary significantly between

islands in the Aleutians (Chapter 2, Major *et al.* ms submitted) thus using survival estimates from Buldir or Kasatochi may provide inaccurate representation of survival at Kiska. With further estimates of adult survival from Kiska, the accuracy of the PVA presented here could be improved.

4.3 RESULTS

4.3.1 Least Auklet Demography

The mean, high and low population projection matrices (Table 4.1) were built using demographic parameters estimated on Kiska Island during 2001 – 2003 and from long-term monitoring on Buldir and Kasatochi Islands. Additional information (proportion of breeding adults) from St. Paul Island, Alaska was used. The mean (best estimate) population projection matrix incorporated only survival and productivity from Kiska and results in a λ of 0.9139, while the high and low matrices were constructed using the survival and productivity estimates from Buldir and Kasatochi Islands and had λ s of 1.2197 and 0.7716.

4.3.2 Population Viability Analysis

4.3.2.1 Perturbation Analysis – Sensitivity Analysis of Mean Population Projection Matrix

The population growth rate for the mean (best estimate; Table 4.1) population projection matrix from Kiska was 0.9139 suggesting that with 2001 – 2003 conditions continuing indefinitely, the population will decrease. Sensitivity and elasticity analysis

of the survival rates revealed that λ was most sensitive to changes in adult survival (P_2), and to changes in the transition probability (G_1), while least sensitive to changes in juvenile survival (P_1) and adult fecundity (F_2 ; Table 4.2, Figure 4.2). When the mean vital rates are graphed within their biological limits it becomes evident that adult survival as measured on Kiska during 2001 – 2002 was approximately average for rat-free colonies, while juvenile survival and the transition probability are below their mean values (Figure 4.3). Sensitivity and elasticity analysis of the mortality rates revealed that λ was most sensitive to changes in juvenile mortality (P_1), and similar to the survival rates, to changes in the transition probability (G_1), while least sensitive to changes in adult mortality (P_2) and fecundity (F_2 ; Table 4.2).

4.3.2.2 Perturbation Analysis – Sensitivity Analysis of Simulated Random Matrices

To determine the sensitivities and elasticities of λ , 500 replications of simulated random population projection matrices between the mean, high and low matrices (Table 4.1) were used to account for variation in demographic parameters and uncertainty. The rankings of elasticities were robust to parameter uncertainty in this model because elasticity values are consistent across the 500 randomly generated matrices (Figure 4.4). Variations that do occur in the vital rates are most likely due to the transition probability (G_1 ; Table 4.3).

4.3.2.3 Management Options

To determine the efficacy of the proposed management scenarios on the population size of Least Auklets breeding at Sirius Point two population projection models were run using 5000 simulations for 30 years (Figure 4.5). The first model, the ‘do nothing’ management option, indicates a 92% reduction in population size in 30 years (from 3 million to 236 523). Similarly, the ‘rat eradication 2’ model indicates a 97% reduction in population size in 30 years (from 3 million to 75 275). While the ‘rat eradication 1’ option, where juvenile survival during the nesting stage is increased to 0.54, reveals a 43% increase in population size in 30 years (from 3 million to 4.3 million).

4.4 DISCUSSION

PVAs are a beneficial tool in conservation biology used to assess managerial options and suggest directions of further research. The accuracy of PVAs are limited by the quality of data used to construct them (Doak *et al.* 1994). Even so they can help assess what parameters need the most accurate estimates and aim the directions of further research. It is important to realize that PVAs cannot predict the future, they should be regarded solely as a tool to help direct what options may be most beneficial to the population in question. PVAs normally are used to assess the viability of small or endangered populations (e.g. Hawaiian Stilt, *Himantopus mexicanus knudseni*, Reed *et al.* 1998; Japanese black bear, *Ursus thibetanus japonicus*, Horino and Miura 2000; Piping Plovers, *Charadrius melodus*, metapopulations, Plissner and Haig, 2000; and

Common Cranes, *Grus grus*, Mathews and Macdonald 2001), but management and conservation of large populations are also necessary to maintain biodiversity and ecosystem health. The goal of this study was to assess the impacts of introduced Norway rats on the large Least Auklet breeding colony located at Sirius Point, Kiska Island, Alaska. I aimed to assess this by performing perturbation analysis on the auklets to understand where future studies should be focused and to assess the viability of two management options (do nothing and control / eradicate Norway rats).

4.4.1 Perturbation Analysis

Sensitivity and elasticity analysis are used to assess which vital rates are most important to changes in λ (van Groenendael 1988). Elasticity analysis is used frequently in PVAs as a tool for conservation and management (e.g. Crouse *et al.* 1987, Doak *et al.* 1994, Wisdom and Mills 1997, Schmutz *et al.* 1997). However, this type of analysis is not without its limitations (see Benton and Grant 1999, Mills *et al.* 1999, de Kroon *et al.* 2000). Care must be exercised when interpreting the results of elasticity analysis because there is a tendency for vital rates with higher means to be identified as the most important rates and because careless interpretation may lead to the implementation of ineffective management plans (Morris and Doak 2002).

For Kiska, perturbation analysis revealed that λ is most sensitive to adult survival and juvenile mortality. However, adult survival was approximately average during 2001 – 2003 and when the rat eradication model was run using adult survival estimates from Buldir a rapid population decline was revealed. However, juvenile mortality was high on

Kiska and managing to reduce juvenile mortality may be a more effective method to increase λ for Least Auklets on Kiska. Nestling mortality and overall juvenile mortality are incorporated in the transition probability and juvenile mortality, so decreased nestling mortality will lead to a decrease in juvenile mortality and the transition probability (the vital rate implicated as the most likely cause of variation in the elasticities and the second most important vital rate to changes in λ) and an increase in λ .

Adult survival on Kiska at one plot over a one year period (0.88) was approximately average for the species (0.87; Jones *et al.* 2002), thus management plans aimed at increasing adult survival do not initially seem to be a viable option. The survival estimate from Kiska is based on the assumption that the single estimate was representative of the entire colony and this may be overly optimistic because high adult mortality was observed in some areas where rats accumulated large hoards of predated Least Auklets (Chapter 3). Further estimates of adult survival at Kiska over more years and at replicated plots would yield a more accurate estimate of survival. Because Least Auklets on Kiska have experienced near reproductive failure in 2001 and 2002 (Chapter 2, Major *et al.* ms submitted) failed breeders were not present on the colony for the duration of those breeding seasons and therefore would have been less vulnerable to predation by rats. If rats were eradicated from Kiska adult survival might increase slightly and because auklet populations are most sensitive to changes in adult survival this could have significant conservation benefits. However, eradication of rats may not have a noticeable impact on adult survival at Kiska because most breeders would not have been exposed to predation because of their failed breeding attempt and subsequent

abandonment of the breeding colony. In terms of conservation of this colony the mortality rates are the most biologically important because of the early abandonment of the colony and the extremely high juvenile mortality observed at Kiska.

Juvenile mortality, as suggested by the elasticities of the mortality matrix, is the vital rate most important to changes in λ . Additionally this vital rate is above its mean and reducing it will lead to a reduction in the transition probability and an increase in λ . Thus, the most viable management option with the current best available auklet demographic data is to decrease juvenile mortality either through controlling the number of rats on the colony early in the breeding season (before rats have had time to multiply after the winter months) or eradicating rats from Kiska Island.

4.4.2 Management Options

Both management options ('do nothing' and 'control / eradicate rats') have potentially serious consequences and require further monitoring to obtain more accurate estimates of survival and productivity before either is implemented. Doing nothing potentially leaves Alaska's largest seabird colony vulnerable to a population crash in three to four decades. Rat eradication and control are both costly and politically complicated options that would not be guaranteed to preserve the auklet population at Kiska if this population is affected by other natural but negative perturbations. Therefore, better quantification of both survival and productivity should be achieved before a final decision on any option is implemented.

It is apparent that without a decrease in nestling mortality, even with the assumptions and limitations of the two models presented here, this colony will experience a severe population decline. Attention needs to be focused on the Kiska Least Auklet population now while it is still high, further quantification of the impacts of rats on this colony and other potential negative factors such as unusually wet, cold weather, outbreaks of parasites, such as *exodes* ticks, and low food availability need to be done now before this population falls below a critical level and recovery efforts become critical and extremely complicated. The reasons behind the low productivity at Kiska need to be identified, and impacts of the introduced rats on juvenile survival (especially during the nestling phase) need to be further studied to determine if rat eradication will decrease juvenile mortality. One proposed method of achieving this would be to perform rat control experiments on representative plots on the auklet colony and monitor and compare juvenile mortality and overall reproductive success on these plots to plots without rat control.

Table 4.1 Summary of the mean, high and low population projection matrices for Least Auklets breeding at Sirius Point, Kiska Island, Alaska.

<i>Mean</i> ¹	<i>High</i> ²	<i>Low</i> ³
$\begin{pmatrix} 0.2138 & 0.6360 \\ 0.1428 & 0.8634 \end{pmatrix}$	$\begin{pmatrix} 0.7215 & 0.7856 \\ 0.2285 & 0.9197 \end{pmatrix}$	$\begin{pmatrix} 0.0868 & 0.4024 \\ 0.0447 & 0.6343 \end{pmatrix}$

Nestling survival: ¹ 0.2534; ² 0.7300; ³ 0.0900 (This study 2001 – 2003, AMNWR unpubl. data).

Adult survival: ¹ 0.8814; ² 0.9756; ³ 0.7705 (This study 2001 – 2003, AMNWR unpubl. data).

Proportion of adults breeding: ¹ 0.6954; ² 0.8269; ³ 0.5365 (Jones 1992).

Table 4.2 Comparison of sensitivity and elasticity analysis of the mean (best estimate) population projection matrices for the survival and mortality rates.

Survival rates

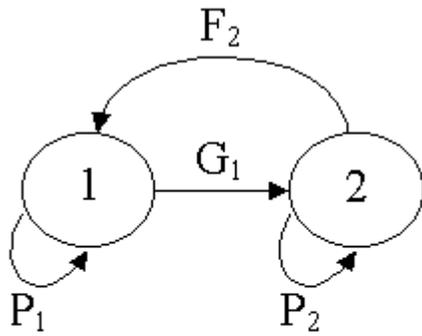
<i>Sensitivities</i>	<i>Elasticities</i>
$\begin{pmatrix} 0.0459 & 0.0523 \\ 0.8369 & 0.9541 \end{pmatrix}$	$\begin{pmatrix} 0.0108 & 0.0351 \\ 0.0351 & 0.9191 \end{pmatrix}$

Mortality rates

<i>Sensitivities</i>	<i>Elasticities</i>
$\begin{pmatrix} 0.9917 & 0.0598 \\ 0.1371 & 0.0083 \end{pmatrix}$	$\begin{pmatrix} 0.9848 & 0.0069 \\ 0.0069 & 0.0014 \end{pmatrix}$

Table 4.3 Summary of the influence of each vital rate on the elasticity values explained by variation in each vital rate for 500 simulated random matrices of Least Auklets on Kiska.

<i>Vital Rate</i>	<i>Minimum Value</i>	<i>Maximum Value</i>	<i>Influence of vital rate on elasticity</i>			
			P1	F2	G1	P2
P1, juvenile survival	0.0846	0.5171	0.61	0.04	0.04	0.16
F2, reproduction of adults	0.4134	0.8067	0.00	0.03	0.03	0.02
G1, transition probability	0.0054	0.2129	0.16	0.81	0.81	0.66
P2, adult survival	0.7684	0.9753	0.08	0.09	0.09	0.10



$$A = \begin{bmatrix} P_1 & F_2 \\ G_1 & P_2 \end{bmatrix}$$

Figure 4.1 Life cycle graph for the stage-classified model and corresponding population projection matrix for Least Auklets at Sirius Point, Kiska Island, Alaska. P_1 represents juvenile survival, F_2 adult fecundity, G_1 the transition probability, and P_2 adult survival.

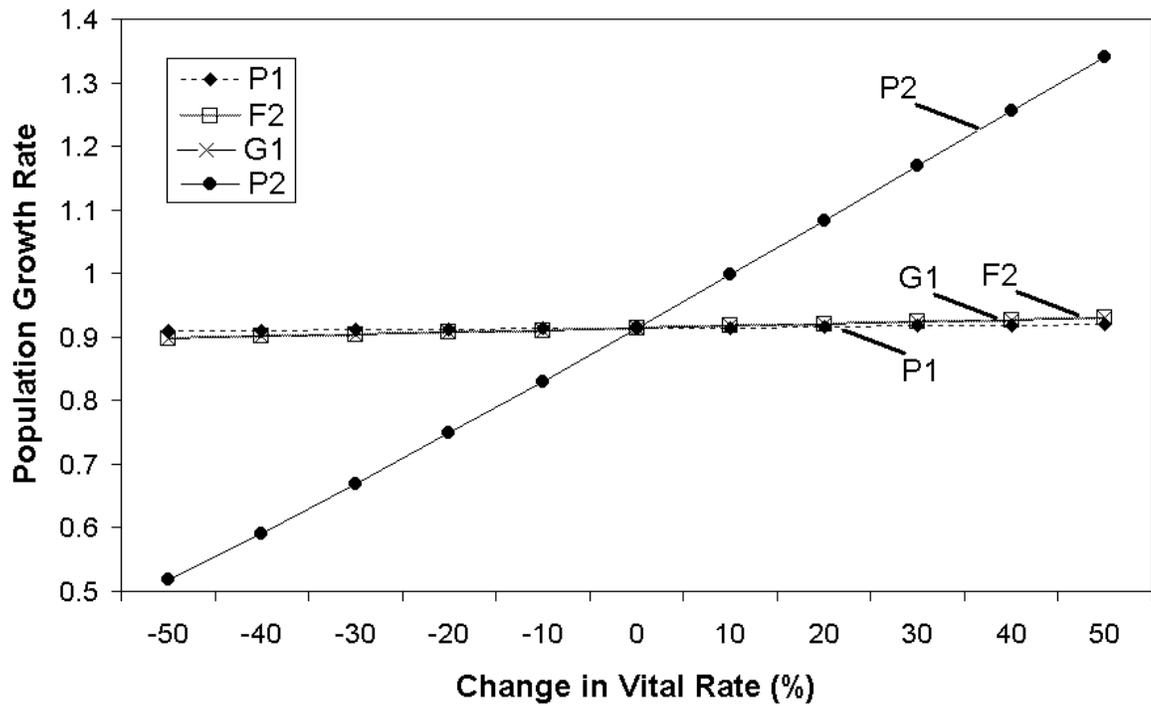


Figure 4.2 Comparison of the sensitivity of λ to changes in the four vital rates from the mean (best estimate) population projection matrix. Where P_1 represents juvenile survival, F_2 adult fecundity, G_1 the transition probability, and P_2 adult survival.

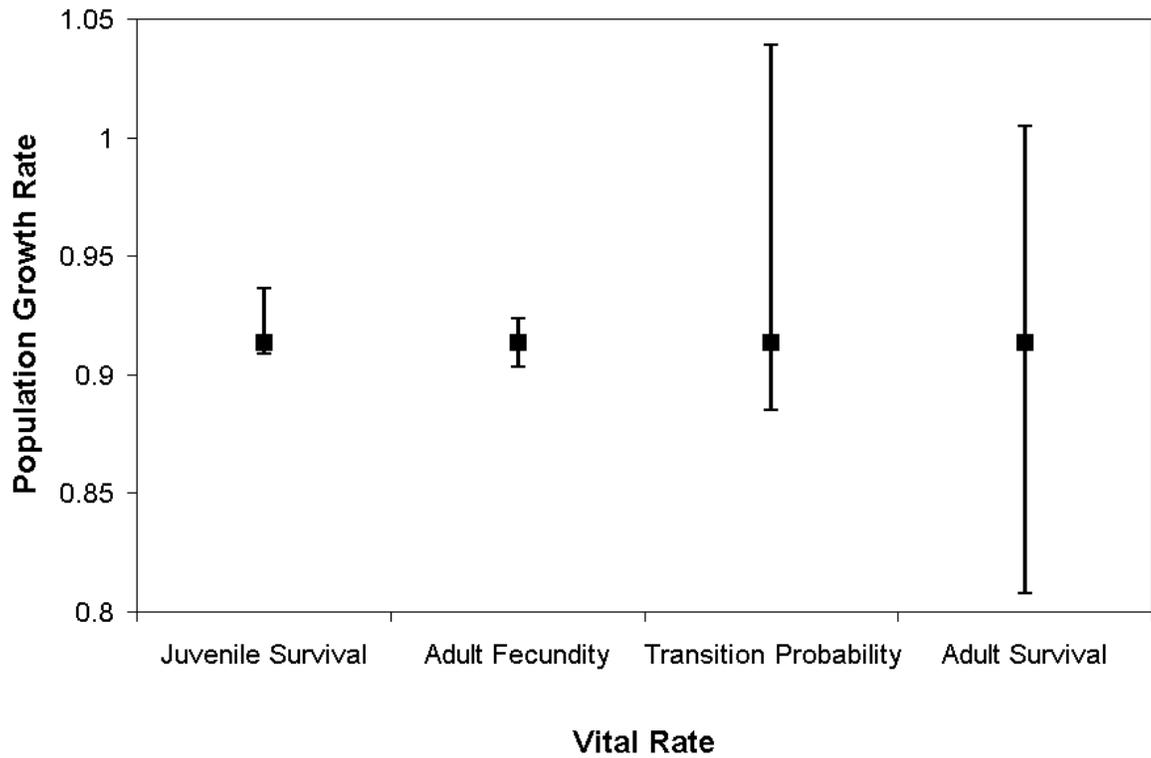


Figure 4.3 Summary of the biological limits of λ for each vital rate showing the current best estimate (from the mean population projection matrix) and maximum and minimum values of λ for each vital rate (from the high and low population projection matrices).

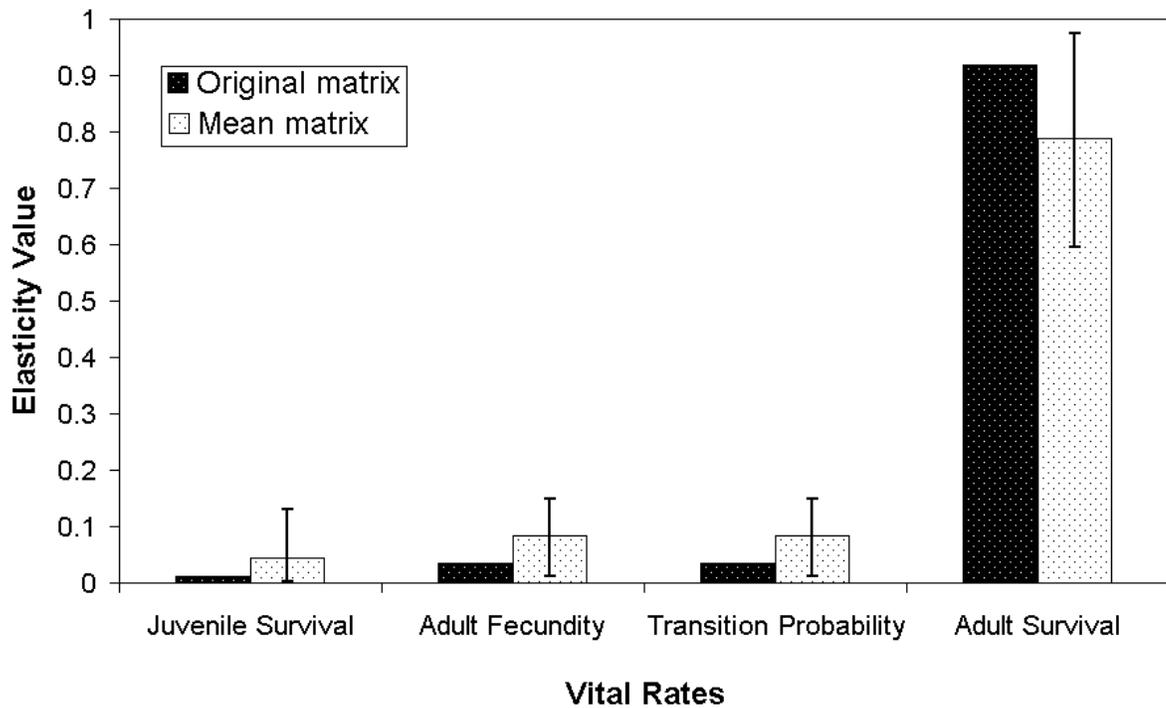


Figure 4.4 Comparison of the elasticity values for the vital rates between the original best estimate matrix shown alongside the mean and 95% confidence intervals around the elasticity estimates from the 500 randomly generated matrices using the maximum and minimum values of the vital rates.

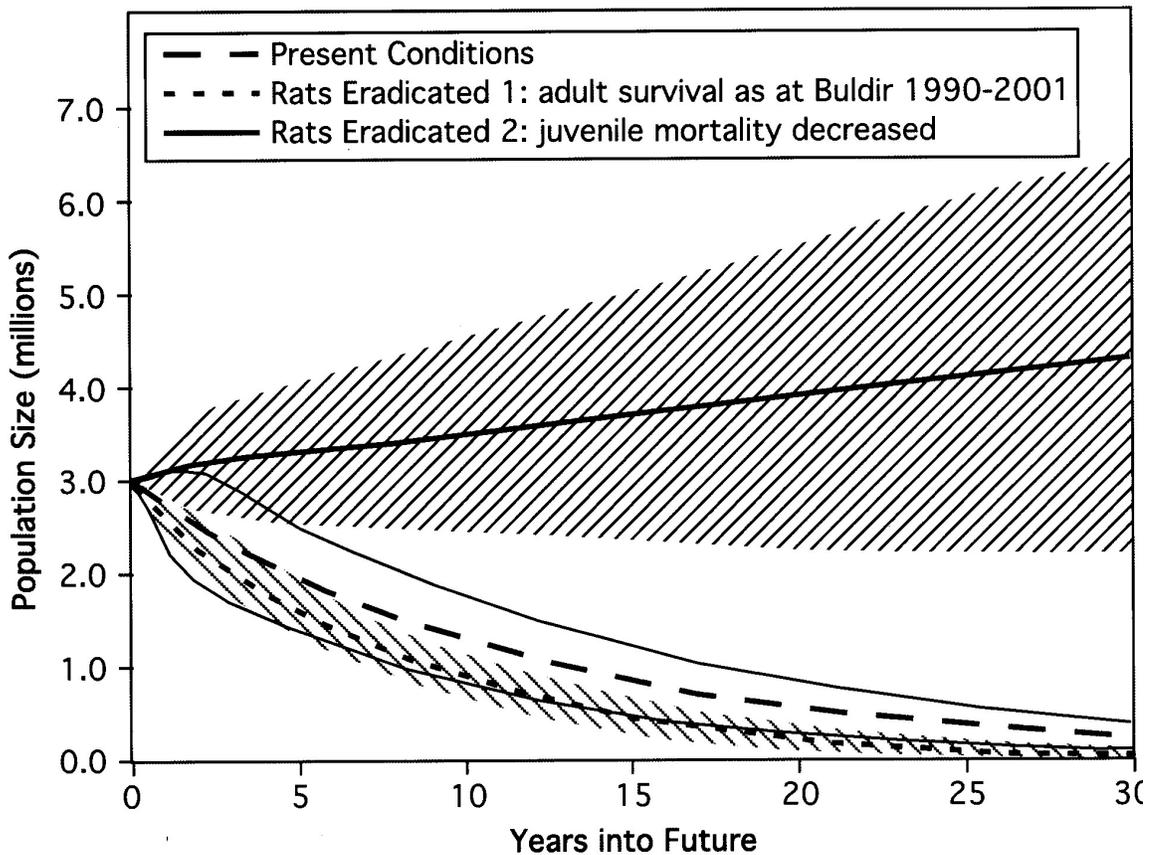


Figure 4.5 Comparison of the projected change in population size of Least Auklets on Kiska, shown with 95% confidence intervals around the mean, under two management options: do nothing (present conditions; confidence intervals shown with solid lines) and control or eradication of rats (rats eradicated 1 – adult survival to Buldir levels; rats eradicated 2 – juvenile mortality at 0.54; confidence intervals shown with shading).

CHAPTER FIVE

SUMMARY

There have been many studies of the impacts of non-indigenous species (NIS) on insular flora and fauna (e.g. Coulter 1984, Jehl and Everett 1985, Bertram 1995, McChesney and Tershy 1998). Other studies have focussed on the restoration of insular species through eradication or control measures (e.g. Taylor *et al.* 2000, Shah 2001). My study differs from all of these and is important for conservation purposes because the Least Auklet (*Aethia pusilla*) population on Kiska Island is still extremely large and at least superficially does not appear to be immediately threatened by introduced Norway rats (*Rattus norvegicus*). Additionally, most studies concerning the impacts of NIS provided limited if any information on the general biology of NIS (e.g. Bertram and Nagorsen 1995, Lee and Yoo 2002). Yet impact assessment and restoration plans rely on knowledge and understanding of all species in question, including the NIS. From a theoretical perspective, my study is important because it is to the best of my knowledge the first to directly measure differences in seabird demography among multiple colony sites with and without NIS and the general biology of both NIS and insular avifauna.

The objectives of my study were to quantify the impacts of introduced Norway rats on the large Least Auklet colony at Sirius Point, Kiska Island, Aleutian Islands, Alaska. This was accomplished by asking three questions pertaining to the biology of both Least Auklets and Norway rats to determine whether a rat control or eradication program should be implemented at Kiska.

Question #1: Does predation by introduced Norway rats decrease Least Auklet reproductive success and interannual survival at Kiska?

During 2001 – 2003 there was extensive evidence of rat predation at the Sirius Point auklet colony site. However, there was little direct evidence that rat predation was the direct cause of failure of my productivity monitoring crevices. Reproductive success at Kiska was extremely low in 2001 and 2002; the lowest ever recorded for the species, suggesting something unique to Kiska during these years. Remarkably, in 2003 Least Auklet reproductive success increased and was similar to that at rat-free Aleutian Islands. Yet, in both 2002 and 2003 Least Auklet chicks on Kiska grew at a slower rate and fledged at a lighter mass and shorter wing chord length than those measured at other Alaskan colonies. In addition, the single annual adult survival estimate for 2001 – 2002 at Kiska (0.88) suggests that rats were not having a detectable impact on adult Least Auklet survival at one study plot during that time period. Taken together, these results suggest that although rats may have a large negative indirect impact on Least Auklet reproductive success in some years, they did not have a measurable impact on Least Auklet adult annual survival based on the limited data available. Poor oceanographic conditions around the island and intra-specific competition resulting from the large auklet population, or a combination of both, could have contributed to poor auklet reproductive success. Yet, I believe that the best explanation for low productivity in 2001 and 2002 is that it was the result of disturbance and predation of Least Auklet adults by Norway rats.

Question #2: What is the distribution of Norway rats on Kiska Island and how does it differ between seasons?

Norway rat sign was found to be abundant in all areas with access to the marine intertidal zone and breeding seabirds at Kiska and decreased in abundance with increasing distance from the intertidal zone and with altitude. During summer, there was a higher proportion of juvenile rats in the population at the Sirius Point auklet colony than at Christine Lake and rats at Sirius Point were found to have a larger mean adult body mass. These two discoveries suggest that Norway rats at the auklet colony subsidized their diet with auklets. In addition, large rat hoards of adult Least Auklets and eggs were found early in the auklet breeding seasons in 2001 and 2002. In 2003 only small rat hoards were found. Rat sign abundance at Sirius Point varied from year to year at Sirius Point. Further studies are required to directly measure the diet and importance of Least Auklets in the diet of Norway rats and to assess the distribution and true abundance of Norway rats on Kiska Island, including rats both on and off the auklet colony and those found inland.

Question #3: Is the auklet colony at Sirius Point threatened with a population collapse, and if so what control measures are required to ensure the survival of this colony?

Under the current best estimate of vital rates (mean vital rates) for 2001 – 2003 my population viability analysis predicted that the population of Least Auklets at Kiska is rapidly decreasing (92% over 30 years). Similarly, under the assumption that rats were eradicated from Kiska and adult survival became similar to that measured on Buldir

Island during 1990 – 2001, the Least Auklet population at Kiska again rapidly decreased (97% over 30 years). However, when a similar model was run assuming that rats were eradicated and were the sole cause of the low reproductive success in 2001 and 2002 the Least Auklet population showed an increase (43% over 30 years). Continued monitoring and assessments of both the direct and indirect impacts of Norway rats needs to be accomplished prior to the implementation of any management plans because there is a large amount of uncertainty in the data used to construct these models. I believe a precautionary approach needs to be employed because of the dire situation indicated by the currently available data. I recommend studies comparing plots with and without rats be developed to observe whether Least Auklet juvenile mortality can be decreased.

The objective of quantifying the impacts of Norway rats at the large Least Auklet colony at Sirius Point, Kiska Island was difficult to achieve. Throughout this study I found little direct evidence of rat predation at my study productivity monitoring crevices or that the auklet breeding failure in 2001 and 2002 resulted directly from rats alone. In addition, there are only three years of data, extreme variations in productivity among these years, one estimate of adult survival from one study plot, and a less than ideal quantification of rat sign abundance and rat distribution at Kiska. However, my data do reveal that something unique and alarming was occurring at Kiska. As the only island that has a Least Auklet monitoring program and rats, Kiska had the lowest auklet reproductive success and slowest chick growth rate; therefore I believe rats are a likely cause of reproductive failure at Sirius Point.

Human disturbance has been shown to negatively impact Least Auklet breeding success (Piatt *et al.* 1990a), thus disturbance by Norway rats (an indirect impact) may also negatively impact their breeding success. Indirect impacts are often difficult to assess (i.e., it was impossible to conclude that an adult Least Auklet that abandoned its chick during brooding, or the death of a chick due to malnourishment, were due to rat activity), but these possible impacts cannot be overlooked. There were examples of circumstantial evidence of indirect impacts of introduced rats, such as an increase in auklet reproductive success in 2003 when the abundance of rat sign was decreased early in the auklet breeding season as compared to 2001 and 2002. Whether the negative impacts of Norway rats are direct or indirect the resulting decreases in reproductive success and survival are the same and equally negative. Indirect impacts cannot be overlooked and need to be quantified at the Sirius Point auklet colony.

As a preliminary assessment of the impacts of Norway rats on Least Auklets breeding at Sirius Point, Kiska Island, this project was a success. Even though few direct impacts were found which make it difficult to hold the rats ultimately responsible for the extremely low reproductive success at Kiska, there is evidence of indirect impacts negatively influencing this population, underlining the need for immediate development of management plans.

The recurring conclusion from this study and highlighted by the perturbation analysis in the population viability analysis was that continued monitoring and reassessments of the Least Auklet population parameters, productivity and survival, are required as mitigation plans are designed and implemented. Future research should focus

on obtaining better estimates of auklet survival and reproductive success at the existing monitoring plots. Given the significance of inter-year variability in the abundance of rat sign and distribution, a rigorous quantitative method to measure both true rat abundance and distribution need to be developed and inland rats must be sampled. In addition, future work at Kiska should include diet analysis using stable isotopes to determine the location of feeding (marine or terrestrial) and the trophic position of Norway rats.

Appendix A Estimates of survival ϕ and recapture rate p from the most parsimonious model [$\phi((\text{Random effects island}) \cdot \text{year}) p(\text{island} \cdot \text{year})$].

<i>Island</i>	<i>Year</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>95% Confidence Interval</i>	
				Lower	Upper
Survival rate					
Buldir	1990	0.861195		0.861195	0.861195
	1991	0.848689		0.848689	0.848689
	1992	0.843875		0.843875	0.843875
	1993	0.860851		0.860851	0.860851
	1994	0.855994		0.855994	0.855994
	1995	0.856331		0.856331	0.856331
	1996	0.862468		0.862468	0.862468
	1997	0.847026		0.847026	0.847026
	1998	0.843942		0.843942	0.843942
	1999	0.848111		0.848111	0.848111
	2000	0.857188		0.857188	0.857188
	2001	0.849348		0.849348	0.849348
Kiska	2001	0.881355	0.033211	0.799445	0.932631
Kasatochi	1996	0.970204		0.970204	0.970204
	1997	0.895487		0.895487	0.895487
	1998	0.87273		0.87273	0.87273
	1999	0.919542		0.919542	0.919542
	2000	0.90394		0.90394	0.90394
	2001	0.78963		0.78963	0.78963
Recapture rate					
Buldir	1990	0.863706	0.078793	0.630538	0.959235
	1991	0.840198	0.07464	0.638789	0.939874
	1992	0.749953	0.082579	0.55854	0.876693

	1993	0.669327	0.082827	0.492916	0.808241
	1994	0.805607	0.072625	0.625455	0.911385
	1995	0.698373	0.071771	0.542834	0.81867
	1996	0.8136	0.060038	0.667663	0.904608
	1997	0.827048	0.049037	0.709492	0.903504
	1998	0.894101	0.038236	0.79279	0.949061
	1999	0.923447	0.036088	0.816015	0.970422
	2000	0.843806	0.048032	0.725622	0.916913
	2001	0.950016	0.033388	0.827309	0.986912
Kiska	2001	0.943584	0.025731	0.866408	0.977342
Kasatochi	1996	0.91753	0.034461	0.820041	0.964493
	1997	0.771728	0.040328	0.683392	0.841147
	1998	0.800598	0.035678	0.721517	0.861532
	1999	0.763191	0.036425	0.68465	0.82711
	2000	0.897138	0.027717	0.828797	0.940168
	2001	0.929218	0.027339	0.853214	0.967373

* Survival rates for Buldir and Kasatochi do not have standard errors because they were estimated using the random effects model.

Appendix B Summary of Norway Rat sign at Kiska during 2001 – 2003.

<i>Date</i>	<i>Location</i>	<i>Comments</i>
24-May-01	Squid Cave	Least Auklet adult with eyes chewed and bites on the neck
2-Jun-01	Old Lava High	Cache #1: Small cache with Least Auklet adults (38), eyes and brains eaten, four with heads missing.
13-Jun-01	Steam Beach	Predated Least Auklet adult
15-Jun-01	Banding plot	Predated Least Auklet adult
26-Jun-01	Camp	Predated Least Auklet adult
13-Jul-01	Near Steam Beach fumerole	Cache #2: Small cache with rotted Least Auklet adults (4).
14-Jul-01	New Lava	Predated Least Auklet adult
14-Jul-01	Banding plot	Least Auklet half eaten embryo with eggshell
18-Jul-01	Valley SW of camp	Predated Least Auklet adult
23-Jul-01	Near Camp	Predated Least Auklet adult (decomposed)
27-Jul-01	Old Lava Low	Predated Least Auklet chick
27-Jul-01	Bob's Plateau	Predated small chick with brain eaten
27-Jul-01	Bob's Plateau	Predated Least Auklet adult with brain eaten (decomposed)
29-Jul-01	Valley SW of camp	Fledging Least Auklet with brain eaten
29-Jul-01	Valley SW of camp	Embryo half eaten with eggshell

26-May-02	Glen Curly, near Steam Beach	Cache #1: Very large cache of fresh Least Auklets (122) including 7 Fork-tailed Storm Petrels, large grass nest located at the end of one of the cache tunnels with a nest of nine rat pups, the adult rat ran out of the tunnel when it was dug up.
30-May-02	Near Squid Cave on the New Lava Dome at Sirius Point	Cache #2: Small cache included Least Auklet adults (34) and eggs. Located under rocks, the whole cache could not be excavated.
4-Jun-02	Near Squid Cave on the New Lava Dome at Sirius Point	Cache #3: Small cache included Least Auklet adults (13) and auklet eggs (33), likely contained more auklets and eggs, but it was inaccessible to. Four of the eggs were Crested Auklet eggs and the rest (29) were Least Auklet eggs.
29-Jun-02	fumerole on New Lava Dome near Steam Beach	Cache #4: Large cache of Least Auklet adults (148) and eggs (6), all auklets were in late stages of decomposition.
17-Jul-02	Above East side of Tangerine Cove	Old Least Auklet carcass with eyes, breast and muscle eaten.
17-Jul-02	Above East side of Tangerine Cove	Fresh, 2-3 day old Least Auklet chick, no apparent injuries, found dead outside of crevice
17-Jul-02	Bay above Sirius Point proper	Predated egg, only head of embryo remains
17-Jul-02	Bay above Sirius Point proper	Old, rat predated egg
17-Jul-02	Bay West of Sirius Point, East of camp	Rat trails in the grass
17-Jul-02	Bay West of Sirius Point, East of camp	Old Least Auklet adult carcass with brain eaten

17-Jul-02	Bay West of Sirius Point, East of camp	Uneaten Crested Auklet egg with tooth marks and puncture
17-Jul-02	Above East end of Tangerine Cove, above camp	Uneaten Least Auklet egg with tooth marks and puncture
17-Jul-02	Above East end of Tangerine Cove, above camp	Predated Least Auklet egg, only head of embryo remains
17-Jul-02	Above East end of Tangerine Cove, above camp	Old Least Auklet adult carcass with brain eaten
17-Jul-02	Above East end of Tangerine Cove, base of cliff	Rat trail through grass
19-Jul-02	On slope behind blind	Least Auklet adult carcass with only the brain eaten
20-Jul-02	Southwest end of New Lava Dome	Fresh rat droppings
20-Jul-02	New Lava Dome, near Steam Beach	Den area, two rats seen near burrow entrances
20-Jul-02	Fumerole, near Steam Beach	Rat droppings all around fumerole
20-Jul-02	Fumerole, near Steam Beach	Rat trails all around fumerole
22-Jul-02	Chick growth plot, New Lava Dome	Least Auklet chick app. 2 weeks old with brain eaten
05-Aug-02	Glen Larry	Least Auklet fledgers (15) with brain eaten, some with breast muscle chewed also

02-Jun-03	Sirius Point Auklet Colony (valley between the New Lava and Old Lava Domes)	Cache 1: Rat cache with >20 adult Least Auklets and >10 Least Auklet eggs (the cache was located under a bolder, we could not excavate the entire cache).
Early-mid Jun-03	Sirius Point Auklet Colony	Sign is not as abundant as 2002, there is some sign of Rats on the colony (we found predated eggs and adults along with droppings). Around camp there is quite a bit of fresh rat sign.
13-Jun-03	Sirius Point Auklet Colony (~50 feet from cache #1)	Cache 2: Rat cache with 8 adult Least Auklets and 11 Least Auklet eggs, all the birds were very decayed.
14-Jun-03	Glen Larry	Extensive digging on the ridge above Glen Larry.
14-Jun-03	Vulcan Point	Extensive digging
14-Jun-03	Cloud Plateau	Digging
14-Jun-03	Christine Lake	Abundant rat sign in the intertidal zone, trails visible in the grass (rat abundance appears similar to that in 2002).
14-16-Jun-03	East Kiska Lake	Footprints found in the sand along the lake's shore
16-Jun-03	Inland between Christine and East Kiska Lakes	Rat sign not abundant
Late Jun–Early Jul-03	Sirius Point Auklet Colony	Abundant rat sign (similar to that in 2002), predated adults, eggs and chicks can be found all over the New Lava Dome and on the beach in front of Camp.
21-Jun-03	Kiska Volcano	Rat sign found (predated auklets, droppings and digging) from Camp up to Lucie's Lounge (~500-600 ft above sea level).

06-Jul-03	Camp	Rat sign (chew marks) found in camp fresh food cache (bread)
Jun–Aug-03	Old Lava Dome	Rat sign not abundant and hard to find
Jul–Aug-03	Camp	Rat droppings and footprints abundant, > five live rats have been seen around camp after dark.
25-26-Jul-03	Christine Lake	Abundant rat sign on beach, diggings around the purple orchids on the hill that leads to cloud plateau.
29-Jul-03	Sirius Point Auklet Colony (in Camp cove beneath Squid Cave and the New Lava Dome)	Cache 3: Rat cache with 5 Least Auklet adults visible (the cache is located under a bolder and could not be accessed)
Late Jul– Early Aug-03	Bob’s Plateau	Lots of predated fledgers
Aug-03	Camp	Predated Crested Auklet adult found behind the weatherport

LITERATURE CITED

- Akçakaya, H.R. 2000. Conservation and management for multiple species: integrating field research and modeling into management decisions. *Environmental Management* 26, Supplement 1: 75-83.
- American Ornithologist Union. 1998. A. O. U. checklist of North American Birds. 7th Edition. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.
- Anderson, D.R., and Burnham, K.P. 1999a. General strategies for the analysis of ringing data. *Bird Study* 46: 261-270.
- Anderson, D.R., and Burnham, K.P. 1999b. Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study* 46: 14-21.
- Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b: 458-473.
- Atkinson, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. *In* Conservation of Island Birds (Moors, P.J. Ed.). International Council for Bird Preservation Technical Publication No. 3: 35-81.
- Atkinson, I.A.E. 2001. Introduced mammals and models for restoration. *Biological Conservation* 99: 81-96.
- Austin, O.L. 1948. Predation by the common rat (*Rattus norvegicus*) in the Cape Cod colonies of nesting terns. *Bird Banding* 29: 60-65.

- Bailey, E.P. 1993. Alaska's alien animals. Pacific Seabird Group Bulletin 20: 5-8.
- Barton, D.C., and Lindquist, K.E. 2003. Biological monitoring in the central Aleutian Islands in 2003: Summary Appendices. U.S. Fish and Wildlife Service report. AMNWR 03/12. Adak, Alaska. 103pp.
- Bédard, J. 1969a. Feeding of the Least, Crested, and Parakeet Auklets around St. Lawrence Island, Alaska. Canadian Journal of Zoology 47: 1025-1050.
- Bédard, J. 1969b. The nesting of the Crested, Least, and Parakeet Auklets on St. Lawrence Island, Alaska. Condor 71: 386-398.
- Bédard, J. and Sealy, S.G. 1984. Moults and feather generations in the Least, Crested and Parakeet Auklets. Journal of Zoology, London 202: 461-488.
- Bent, A.C. 1963. Life histories of North American diving birds. Dover Publ. New York. pp. 120.
- Benton, T.G. and Grant, A. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution 14: 467-471.
- Bertram, D.F. 1995. The roles of introduced rats and commercial fishing in the decline of Ancient Murrelets on Langara Island, British Columbia. Conservation Biology 9: 865-872.
- Bertram, D.F. and Nagorsen, D. W. 1995. Introduced rats, *Rattus* spp., on the Queen Charlotte Islands: implications for seabird conservation. Canadian Field-Naturalist 109: 6-10.
- Bertram, D.F., I. L. Jones, E. Cooch, and F. Cooke. 2000. Survival rates of Cassin's and Rhinoceros Auklets at Triangle Island, British Columbia. Condor 102: 155-162.

- Bindra, D. 1948a. The nature of motivation for hoarding food. *Journal of Comparative Physiological Psychology* 41: 211-218.
- Bindra, D. 1948b. What makes rats hoard? *Journal of Comparative Physiological Psychology* 41: 397-402.
- Birkhead, T.R. and Nettleship, D.N. 1981. The adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. *Ecology* 63: 300-306.
- Boddington, D. 1960. Unusual mortality of young puffins on St. Kilda, 1959. *Scottish Birds* 1: 218-220.
- Boyce, M.S. 1992. Population viability analysis. *Annual Review of Ecological Systems* 23: 481-506.
- Breault, A.M. and Cheng, K.M. 1988. Surplus killing of Eared Grebes, *Podiceps nigricollis*, by Mink, *Mustela vison*, in Central British Columbia. *Canadian Field-Naturalist* 102: 738-739.
- Burnham, K.P. and Anderson, D.R. 1998. Model selection and inference -a practical information-theoretic approach. Spring-Verlag, New York.
- Byrd, G.V., Trap, J.L., and Zeillemaker, C.F. 1994. Removal of introduced foxes: A case study in restoration of native birds. *Transactions of the 59th North American Wildlife & Natural Resources Conference*.
- Cabanac, M. 1985. Influence of food and water deprivation on the behaviour of the White rat foraging in a hostile environment. *Physiology and Behaviour* 35: 701-709.

- Cabanac, M. and Swiergiel, A.H. 1989. Rats eating and hoarding as a function of body weight and cost of foraging. *American Journal of Physiology* 257: R952-R957.
- Carbyn, L.N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. *Journal of Wildlife Management* 47: 963-976.
- Carlquist, S. 1965. *Island life: A natural history of the islands of the world*. The Natural History Press, New York.
- Carlquist, S. 1974. *Island Biology*. Columbia University Press. New York.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer, Sunderland, Mass.
- Chaloupka, M. 2002. Stochastic simulation modelling of southern Great Barrier Reef Green turtle population dynamics. *Ecological Modelling* 148: 79-109.
- Chapuis, J.L., Bousset, P. and Barnaud, G. 1994. Alien mammals, impact and management in the French subantarctic islands. *Biological Conservation* 67: 97-104.
- Cooch, E.G., and G.W. White. 2001. *Using MARK – a gentle introduction*, 2nd Ed. Available at <http://www.phipot.org/software/mark/docs/book/>
- Coulson, T., Mace, G.M., Hudson, E., and Possingham, H. 2001. The use and abuse of population viability analysis. *Trends in Ecology and Evolution* 16: 219-221.
- Coulter, M.C. 1984. Seabird conservation in the Galapagos Islands, Ecuador. *In Status and Conservation of the World's Seabirds* (Croxall, J.P., Evans, P.G.H. and Schreiber, R.W., Eds.) International Council for Bird Preservation Technical Publication 2: 237-244.

- Cowie, R.H. 2001. Invertebrate invasions on Pacific Islands and the replacement of unique native faunas: a synthesis of the land and freshwater snails. *Biological Invasions* 3: 119-136.
- Crooks, J.A. 2002. Characterising ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97: 153-166.
- Crouse, D.T., Crowder, L.B. and Caswell, H. 1987. A stage-based population model for Loggerhead Sea Turtles and implications for conservation. *Ecology* 68: 1412-1423.
- Cruz, J.B. and Cruz, F. 1987. Conservation of the Dark-rumped Petrel *Pterodroma phaeopygia* in the Galapagos Islands, Ecuador. *Biological Conservation* 42: 303-311.
- Day, R.H. and Byrd, G.V. 1989. Food habits of the Whiskered Auklet at Buldir Island, Alaska. *Condor* 91: 65-72.
- Day, R.H., Lawhead, B.E., Early, T.J., and Rhode, E.B. Results of marine bird and mammal survey of the western Aleutian Islands, summer 1978. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Aleutian Islands National Wildlife Refuge, Unpublished Administrative Report.
- De Forest, L.N. and Gaston, A.J. 1996. The effect of age on the timing of breeding and reproductive success in the Thick-billed Murre. *Ecology* 77: 1501-1511.
- de Kroon, H., Plaisier, A., van Groenendael, J., and Caswell, H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427-1431.

- de Kroon, H., van Groenendael, J., and Ehrlén, J. 2000. Elasticities: A review of methods and model limitations. *Ecology* 81: 607-618.
- DelGiudice, G.D. 1998. Surplus killing of White-tailed deer by Wolves in Northcentral Minnesota. *Journal of Mammalogy* 79: 227-235.
- Diamond, J. 1985. Rats as agents of extermination. *Nature* 318: 602-603.
- Doak, D., Kareiva, P. and Klepetka, B. 1994. Modelling population viability for the Desert tortoise in the Western Mojave Desert. *Ecological Applications* 4: 446-460.
- Dowding, J.E. and Murphy, E.C. 2001. The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. *Biological Conservation* 99: 47-64.
- Drever, M.C. and Harestad, A.S. 1998. Diets of Norway rat, *Rattus norvegicus*, on Langara Island, Queen Charlotte Islands, British Columbia: Implications for conservation of breeding seabirds. *Canadian Field-Naturalist* 112: 676-683.
- Ebbert, S. 2000. Successful eradication of introduced Arctic foxes from large Aleutian Islands. *Proceedings of the 19th Vertebrate Pest Conference*: 127-132.
- Ellner, S.P., Fieberg, J., Ludwig, D., and Wilcox, C. 2002. Precision of population viability analysis. *Conservation Biology* 16: 258-261.
- Endler, 1986. *Natural selection in the wild. Monographs in Population Biology No. 21*, Princeton University Press, Princeton, N.J.
- Fantino, M. and Cabanac, M. 1980. Body weight regulation with a proportional hoarding response in the rat. *Physiology and Behaviour* 24: 939-942.

- Fritts, T.H. and Rodda, G.H. 1998. The role introduced species in the degradation of island ecosystems: A case history of Guam. *Annual Review of Ecological Systems* 29: 113-140.
- Gaston, A.J. and Jones, I.L. 1998. The Auks: Alcidae. *Bird Families of the World*, No. 4. Oxford University Press, New York.
- Grant, P.R. 1972. Centripetal selection and the house sparrow. *Systematic Zoology* 21: 23-30.
- Greenway, J.C., Jr. 1967. *Extinct and vanishing birds of the world*. Dover Publ. Inc. Toronto. pp. 520.
- Hamilton, S. and Moller H. 1995. Can PVA models using computer packages offer useful conservation advice? Sooty Shearwaters *Puffinus griseus* in New Zealand as a case study. *Biological Conservation* 73: 107-117.
- Hansen, D.M., Olesen, J.M., and Jones, C.G. 2002. Trees, birds and bees in Mauritius: exploitative competition between introduced honeybees and endemic nectivorous birds? *Journal of Biogeography* 29: 721-734.
- Harris, M.P. 1970. The biology of an endangered species, the Dark-rumped Petrel (*Pterodroma phaeopygia*), in the Galapagos Islands. *Condor* 72: 76-84.
- Harrison, C.S., Naughton, M.B. and Fefer, S.I. 1984. The status and conservation of seabirds in the Hawaiian archipelago and Johnston atoll. *In* Status and Conservation of the World's Seabirds (Croxall, J.P., Evans, P.G.H. and Schreiber, R.W., Eds.). International Council for Bird Preservation Technical Publication 2: 513-526.

- Hedgren, S. 1980. Reproductive success of Guillemots *Uria aalge* on the island of Stora Karlsö. *Ornis Fennica* 57: 49-57.
- Heppell, S.S., Caswell, H. and Crowder, L.B. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81: 654-665.
- Horino, S. and Miura, S. 2000. Population viability analysis of a Japanese Black bear population. *Population Ecology* 42: 73-44.
- Hunt, G.L., Jr. 1997. Physics, zooplankton, and the distribution of Least Auklets in the Bering Sea - a review. *ICES Journal of Marine Science* 54: 600-607.
- Hussell, D.J.T. 1972. Factors affecting clutch size in arctic passerines. *Ecological Monographs* 42: 317-364.
- Imber, M.J. 1975. Petrels and predators. *International Council for Bird Preservation Bulletin* 12: 260-263.
- International Council for Bird Preservation. 1984. Priorities for seabird conservation and associated research: Recommendations of the ICBP seabird specialist group. *In: Status and Conservation of the World's Seabirds* (Croxall, J.P., Evans, P.G.H. and Schreiber, R.W. Eds.) *International Council for Bird Preservation Technical Publication* 2: 771-778.
- Jedrezejewski, B. and Jedrezejewski, W. 1989. Seasonal surplus killing as hunting strategy of the weasel *Mustela nivalis* – test of a hypothesis. *Acta Theriologica* 34: 347-359

- Jehl, J.R., Jr. and Everett, W.T. 1985. History and status of the avifauna of Isla Guadalupe, Mexico. *Transactions of the San Diego Society of Natural History* 20: 313-336.
- Jochelson, W. 1968. History, ethnology and anthropology of the Aleut. Anthropological publ. Netherlands.
- Jones, A.G., Chown, S.L. and Gaston, K.J. 2003. Introduced house mice as a conservation concern on Gough Island. *Biodiversity and Conservation* 12: 2107-2119.
- Jones, C.G., Lawton, J.H., and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373-386.
- Jones, C.G., Lawton, J.H., and Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946-1957.
- Jones, I.L. 1990. Plumage variability functions for status signalling in Least Auklets. *Anim. Behav.* 39: 967-975.
- Jones, I.L. 1992a. Colony attendance of Least Auklets at St. Paul Island, Alaska: implications for population monitoring. *Condor* 94: 93-100.
- Jones, I. L. 1992b. Factors affecting survival of adult Least Auklets (*Aethia pusilla*) at St. Paul Island, Alaska. *Auk* 109: 576-584.
- Jones, I.L. 1993a. Least Auklet (*Aethia pusilla*). *In* The Birds of North America, No. 69 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

- Jones, I.L. 1993b. Sexual differences in bill shape and external measurements of Crested Auklets. *Wilson Bulletin* 105: 525-529.
- Jones, I.L., Hunter, F.M., and Robertson, G.J. 2002. Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. *Oecologia* 133: 38-44.
- Jones, I.L. and Montgomerie, R. 1991. Mating and remating of Least Auklets (*Aethia pusilla*) relative to ornamental traits. *Behavioral Ecology* 2: 249-257.
- Jones, I.L. and Montgomerie, R. 1992. Least Auklet ornaments: do they function as quality indicators? *Behavioural Ecology and Sociobiology* 30: 43-52.
- Jouventin, P., Bried, J., and Micol, T. 2003. Insular bird populations can be saved from rats: a long-term experimental study of White-chinned Petrels *Procellaria aequinoctialis* on Ile de la Possession (Crozet archipelago). *Polar Biology* 26: 371-378.
- Kaufman, L. 1992. Catastrophic change in species-rich freshwater ecosystems: the lessons of Lake Victoria. *Bioscience* 42: 846-858.
- Kelly, M.J. and Durant, S.M. 2000. Viability of the Serengeti Cheetah population. *Conservation Biology* 14: 786-797.
- Kepler, C.B. 1967. Polynesian rat predation on nesting Laysan Albatrosses and other Pacific seabirds. *Auk* 84: 426-430.
- Key, G., Fielding, A.H., Goulding, M.J., Holm, R.S., and Stevens-Woods, B. 1998. Ship rats *Rattus rattus* on the Shiant Islands, Hebrides, Scotland. *Journal of Zoology, London* 245: 228-233.

- King, W.B. 1980. Ecological basis of extinction in birds. Proceedings of the Berlin International Ornithological Congress 17: 905-911.
- King, W.B. 1985. Island birds: will the future repeat the past? *In*: Conservation of Island Birds (Moors, P.J., Ed.). International Council for Bird Preservation Technical Publication No. 3: 3-15.
- Kitchell, J.F., Schindler, D.E., Ogutu-Ohwayo, R., and Reinthal, P.N. 1997. The Nile perch in Lake Victoria: Interactions between predation and fisheries. *Ecological Applications* 7: 653-664.
- Knudtson, E.P. and Byrd, G.V. 1982. Breeding biology of Crested, Least, and Whiskered Auklets on Buldir Island, Alaska. *Condor* 84: 197-202.
- Kruuk, H. 1972. Surplus killing by carnivores. *Journal of Zoology, London* 166: 233-244.
- Landry, S.O., Jr. 1970. The Rodentia as omnivores. *Quarterly Review of Biology* 45: 351-372.
- Laughlin, W.S. 1980. Aleuts: Survivors of the Bering land bridge. Holt, Rinehart and Winston. New York.
- Lawton, J.H. 1994. What do species do in ecosystems? *Oikos* 71: 367-374.
- Lebreton, J-D, Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67-118.
- Lee, K.-G. and Yoo, J.-C. 2002. Breeding population of Streaked Shearwaters (*Calonectris leuomelas*) and the effect of Norway rat (*Rattus norvegicus*)

- predation on Sasudo Island. *Journal of Yamashina Institute of Ornithology* 33: 142-147.
- Lefkovitch, L.P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* 21: 1-18.
- Lensink, C.J. 1984. The status and conservation of seabirds in Alaska. *In*: Croxall, J.P., Evans, P.G.H. and Schreiber, R.W. (Eds.): *Status and Conservation of the World's Seabirds*. International Council for Bird Preservation Technical Publication 2: 13-27.
- Li, D. and Jiang, Z. 2002. Population viability analysis for the Prezewalski's Gazelle. *Russian Journal of Ecology* 33: 115-120.
- Licklider, L.C. and Licklider, J.C.R. 1950. Observations on the hoarding behaviour of rats. *Journal of Comparative Physiological Psychology* 43: 129-134.
- Lindenmayer, D.B. and Lacy, R.C. 2002. Small mammals, habitat patches and PVA models: a field test of model predictive ability. *Biological Conservation* 103: 247-265.
- Lindenmayer, D.B., Possingham, H.P., Lacy, R.C., McCarthy, M.A., and Pope, M.L. 2003. How accurate are population models? Lessons from landscape-scale tests in a fragmented system. *Ecology Letters* 6: 41-47.
- Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8: 133-136.
- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80: 298-310.

- MacArthur, R.H. and Wilson E.O. 2001. The theory of island biogeography. Princeton University Press. Princeton.
- MacLennan, D., Ferguson, J. and Buxton, N. 2000. *Rattus rattus* on the Shiant Islands: a study of distribution and abundance. Hebridian Naturalist 13: 7-17.
- Major, H.L., Jones, I.L., Byrd, G.V., and Williams, J.C. ms submitted. Assessing the effects of introduced Norway rats (*Rattus norvegicus*) on reproductive performance and survival of Least Auklets (*Aethia pusilla*) at Kiska Island, Alaska during 2001 – 2003. Auk
- Marmontel, M., Humphrey, S.R., and O’Shea, T.J. 1996. Population viability analysis of the Florida manatee (*Trichechus manatus latirostris*), 1976-1991. Conservation Biology 11: 467-481.
- Mathews, F. and Macdonald, D.W. 2001. The sustainability of the common crane (*Grus grus*) flock breeding in Norfolk: insights from simulation modelling. Biological Conservation 100: 323-333.
- McChesney, G.J. and Tershy, B.R. 1998. History and status of introduced mammals and the impacts on breeding seabirds on the California Channel and Northwestern Baja California Islands. Colonial Waterbirds 21: 335-347.
- McDonald, D.B. and Caswell, H. 1993. Matrix methods for avian demography, *In* Current Ornithology, Vol. 10 (Power, D.M., Ed.), Plenum Press, New York, pp. 139-185.
- Miller, F.L., Gunn, A., and Broughton, E. 1985. Surplus killing as exemplified by wolf predation on new-born caribou. Canadian Journal of Zoology 63: 295-300.

- Miller, T.P., McGimsey, R.G., Richter, D.H., Riehle, J.R., Nye, C.J., Yount, M.E., and Dumoulin, J.A. 1998. Catalogue of the Historically Active Volcanoes of Alaska. U.S. GEOLOGICAL SURVEY Open-File Report 98-582, 104 pages, 102 figures.
- Mills, L.S., Doak, D.F. and Wisdom, M.J. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* 13: 815: 829.
- Moors, P.J. 1990. Norway rat. *In: The handbook of New Zealand mammals.* (King, C.M., Ed.) Oxford University Press, Auckland. pp. 192-206.
- Moors, P.J. and Atkinson, I.A.E. 1984. Predation on seabirds by introduced animals, and factors affecting its severity. *In: Status and Conservation of the World's Seabirds* (Croxall, J.P., Evans, P.G.H. and Schreiber, R.W. Eds.). International Council for Bird Preservation Technical Publication 2: 667-690.
- Morris, W.F. and Doak, D.F. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland, Mass.
- Murie, O.J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. *North American Fauna*, Volume 61, U.S. Fish and Wildlife Service.
- Okansen, T., Okansen, L., and Fretwell, S.D. 1985. Surplus killing in the hunting strategy of small predators. *American Naturalist* 126: 328-346.
- Olds, R.J. and Olds, J.R. 1979. A colour atlas of the rat dissection guide. Wolfe Medical Public. Ltd. Italy.
- Palmer, V. and Pons, G.X. 2001. Predicting rat presence on small islands. *Ecography* 24: 121-126.

- Patterson, B.R. 1994. Surplus killing of White-tailed Deer, *Odocoileus virginianus*, by Coyotes, *Canis latrans*, in Nova Scotia. *Canadian Field-Naturalist* 108: 484-487.
- Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. *American Zoologist* 34: 134-144.
- Pearson, T.G., Burroughs, J., Forbush, E.H., Herbert, K.J., Finley, W.L., Nichols, L.N., Gladden, G., and Burdick, J.E. 1936. *Birds of America*. Garden City Publ. Company, Inc. New York.
- Pergrams, O.R.W., Lacy, R.C. and Ashley, M.V. 2000. Conservation and management of Anacapa Island Deer mice. *Conservation Biology* 14: 819-832.
- Perras, G.R. 2003. *Stepping stones to nowhere: the Aleutian Islands, Alaska, and American Military Strategy, 1987-1945*. UBC Press. Vancouver, BC.
- Pfab, M.F. and Witkowski, E.T.F. 2000. A simple population viability analysis of the critically endangered *Euphorbia clivicola* R.A. Dyer under four management scenarios. *Biological Conservation* 96: 263-270.
- Piatt, J.F., Roberts, B.D., Lidster, W.W., Wells, J.L., and Hatch, S.A. 1990a. Effects of human disturbance on breeding Least and Crested Auklets at St. Lawrence Island, Alaska. *Auk* 107: 342-350.
- Piatt, J.F., Roberts, B.D. and Hatch, S.A. 1990b. Colony attendance and population monitoring of Least and Crested Auklets on St. Lawrence Island, Alaska. *Condor* 92: 97-106.
- Plissner, J.H. and Haig, S.M. 2000. Viability of piping plover *Charadrius melodus* metapopulations. *Biological Conservation* 92: 163-173.

- Possingham, H.P., Lindenmayer, D.B. and Norton, T.W. 1993. A framework for the improved management of threatened species based on population viability analysis (PVA). *Pacific Conservation Biology* 1: 39-45.
- Pradel, R., Rioux, N., Tamisier, A., and Lebreton, J-D. 1997. Individual turnover among wintering Teal in Camargue: a mark-recapture study. *Journal of Wildlife Management* 61: 816-821.
- Prévot-Juilliard, A.C., Lebreton, J-D., and Pradel, R. 1998. Re-evaluation of adult survival of Black-headed Gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *Auk* 115: 85-95.
- Reed, J.M., Elphick, C.S., and Oring, L.W. 1998. Life history and viability analysis of the endangered Hawaiian Stilt. *Biological Conservation* 84: 35-45.
- Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48: 978-983.
- Roby, D.D. and Brink, K.L. 1986. Breeding biology of Least Auklets on the Pribilof Islands, Alaska. *Condor* 88: 336-346.
- Roby, D.D., Place, A.R. and Ricklefs, R.E. 1986. Assimilation and deposition of wax esters in planktivorous seabirds. *Journal of Experimental Zoology* 238: 29-41.
- Roots, C. 1976. *Animal Invaders*. Universe Books. New York. Ch. 3.
- Russel, R.W., Harrison, N.M. and Hunt, G.L.Jr. 1999. Foraging at a front: hydrography, zooplankton, and avian planktivory in the northern Bering Sea. *Marine Ecology Progress Series* 182: 77-93

- Savidge, J.A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68: 660-668.
- Schmutz, J.A., Rockwell, R.F. and Petersen, M.R. 1997. Relative effects of survival and reproduction on the population dynamics of Emperor Geese. *Journal of Wildlife Management* 61: 191-201.
- Sealy, S. G. 1968. A comparative study of the breeding ecology and timing in plankton-feeding alcids on St. Lawrence Island, Alaska. M.Sc. dissertation, University of British Columbia, Vancouver.
- Sealy, S.G. 1973. Adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. *Ornis Scandinavica* 4: 113-121.
- Shah, N.J. 2001. Eradication of alien predators in the Seychelles: an example of conservation action on tropical islands. *Biodiversity and Conservation* 10: 1219-1220.
- Shrader-Frechette, K. 2001. Non-indigenous species and ecological explanation. *Biology and Philosophy* 16: 507-519.
- Sowls, A.O., Hatch, S.A., and Lensink, C.J. 1978. Catalogue of Alaskan seabird colonies. U.S. Dept. Interior, U.S. Fish and Wildlife Service, FWS/OBS-78/78.
- Stapp, P. 2002. Stable isotopes reveal evidence of predation by ship rats on seabirds on the Shiant Islands, Scotland. *Journal of Applied Ecology* 39: 831-840.
- Stapp, P. and Hayward, G.D. 2002. Effects of introduced piscivore on native trout: insights from a demographic model. *Biological Invasions* 4: 299-316.

- Steadman, D.W. 1995. Prehistoric extinctions on Pacific island birds: biodiversity meets zooarcheology. *Science*, 267: 1123-1131.
- Steadman, D.W. 1999. The biogeography and extinction of megapodes in Oceania. *Zoologische Verhandelingen (Leiden)* 327: 7-21.
- Steadman, D.W., Pregill, G.K., and Burley D.V. 2002. Rapid prehistoric extinction of iguanas and birds in Polynesia. *Proceedings of the National Academy of Science USA* 99: 3673-3677.
- Takahashi, L.K. and Lore, R.K. 1980. Foraging and food hoarding of wild *Rattus norvegicus* in an urban environment. *Behavioural and Neural Biology*. 29: 527-531.
- Taylor, B.L. 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology* 9: 551-558.
- Taylor, R.H., Kaiser, G.W., and Drever M.C. 2000. Eradication of Norway rats for recovery of seabird habitat on Langara Island, British Columbia. *Restoration Ecology* 8: 151-160.
- Thorsen, M., Shorten, R., Lucking, R., and Lucking, V. 2000. Norway rats (*Rattus norvegicus*) on Frégate Island, Seychelles: the invasion; subsequent attempts and implications for the island's fauna. *Biological Conservation* 96: 133-138.
- Towns, D.R. and Ballantine, W.J. 1993. Conservation and restoration of New Zealand ecosystems. *Trends in Ecology and Evolution* 8: 452-457.

- Towns, D.R., Parrish, G.R., Westbrooke, I. 2003. Inferring vulnerability to introduced predators without experimental demonstration: Case study of Suter's Skink in New Zealand. *Conservation Biology* 17: 1361-1371.
- van Groenendael, J., de Kroon, H., and Caswell, H. 1988. Projection matrices in population biology. *Trends in Ecology and Evolution* 3: 687-690.
- Vermeij, G.J. 1996. An agenda for invasion biology. *Biological Conservation* 78: 3-9.
- Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57: 7-13.
- White, G.C. and Burnham, K.P. 1999. Program MARK - survival estimation from populations of marked animals. *Bird Study* 46: 120-139.
- Williams, G.C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.
- Williamson, M. 1996. *Biological invasions*. Chapman & Hall. London.
- Williamson, M. and Fitter, A. 1996. The varying success of invaders. *Ecology* 77: 1661-1666.
- Wisdom, M.J. and Mills, L.S. 1997. Sensitivity analysis to guide population recovery: Prairie-Chickens as an example. *Journal of Wildlife Management* 61: 302-312.
- Ydenberg, R.C., Clark, C.A., and Harfenist, A. 1995. Intraspecific fledging mass variation in the Alcidae, with special reference to the seasonal fledging mass decline. *American Naturalist* 145: 412-433.