University of Alberta

Intraspecific cache pilferage by larder-hoarding red squirrels (*Tamiasciurus hudsonicus*) in Kluane, Yukon.

by

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A thesis submitted to the Faculty of Graduate Studies and Research

in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences

Fall 2010

Edmonton, Alberta

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ABSTRACT

Pilfering is thought to play a role in the evolution of scatter-hoarding strategies; but is not well understood in larder-hoarding animals. I studied intraspecific pilfering in red squirrels in Kluane, YT, Canada. The purpose of this project was to estimate the natural rate of cache pilferage, and to examine variation in pilfering behaviour. Results from experimental removal of territory owners, suggested that younger squirrels with smaller food caches were more likely to pilfer when given the opportunity. Survival over-winter was dependent on the number of cones cached and pilfering squirrels were less likely to survive. Using a mark-recapture study of marked cones I found that few individuals (14%) did any pilfering and stolen cones represented only 0.3% of total cones cached. It is clear that pilfering occurs at a much lower rate in Kluane than reported for red squirrels in other regions, and is less than rates reported for scatter-hoarding species.

ACKNOWLEDGEMENT

I would like to thank my supervisor Stan for allowing me the independence to explore and develop my own research interests and for the amazing opportunity to work at squirrel camp and in the Yukon. His guidance and advice were invaluable in completing this thesis. Thank you also to my committee, Pete Hurd and Colleen Cassidy St. Clair, who provided helpful advice. Without some of your ideas (especially the removal experiment) my thesis may have been a rather dull document. Thanks so much to Ainsley Sykes who has been an invaluable resource for coordinating field work and was always extremely helpful when searching out squirrel data. Also thank you to Erin Bayne for help with the finer points of sigmoidal curves, SD, and AIC.

Thank you to Ben Dantzer, Ryan Taylor, and Quinn Fletcher who taught me the ropes up at Squirrel Camp and gave me a crash course in what it means to be Squirreler. Thanks to Jamie Gorrell, Jeff Lane, and Mark Andruskiw who got me started on all this stealing business and provided valuable input into my first attempts at proposals and field planning. Heartfelt thanks to Meghan Larivee and Julia Shonfield who not only contributed many ideas, but were also amazing friends. This project would have been impossible without the tireless efforts of all the field techs that have monitored the grids since the very beginning. Special thanks to the 2008 and 2009 crews who made my time in squirrel camp a truly exceptional field experience, which I am sure I will reminisce about forever. Kat, Issac, Cate, Beth, Bastian, Christina, Jo, and Emily you guys are truly amazing people. Special thanks to Jen Yip who volunteered her time to help me search out thousands of needles in several haystacks. Maria Diebolt was the most amazing field assistant a person could ask for and a truly great friend. Thanks

Maria for filling up every day with your incredible enthusiasm, and for surviving all of my quirks in those weeks of isolation. Oh and thank you to all those squirrels – especially the ones who stole cones – without them I would have no data.

A hundred million thank-you's to Justin Hanish and Eva Kuczynski who answered my pestering questions and put up with my constant interruptions in the office. Thanks also to Stan Clan for expanding my ecological toolbox far outside the scope of stealing squirrels and providing valuable contributions to my project. Katie, Helen, Megan, Jen, Justin, Brianne, and Mark – thanks for teaching me Edmonton *can* be a fun place. Thank you especially to Francoise who has been a great friend, and who put up with living with me these last couple of years and seems to have survived my antics relatively unscathed.

To my Mom and Dad who never stopped encouraging me and gave me the foundation to reach where I am – thank you does not quite seem adequate. Kathy, Aunt Linda and Uncle Dave, thank you for taking me into the wilderness and fostering my love of the outdoors each in your own unique way. Finally to Jesse, thank you for sticking by me through all of this. I truly could not have accomplished what I have without your unwavering love and support. And just so you can brag about it to all our friends:

I, Jenna Donald, dedicate this thesis to Michael Jesse Lamb B.A. FCIP.

This project was supported by research grants from the Northern Scientific Training Program and a NSERC Discovery grant to SB.

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INTRODUCTION AND THESIS OVERVIEW

RESOURCES AND HOARDING STRATEGIES

The availability of resources plays a primary role in the ecology of organisms. Fluctuations in the availability of food resources can ultimately affect individual behaviour, population, and community dynamics (Holt 2008, Yang et al. 2008). Resources in many ecosystems arrive in pulses: mast production of seeds and flowers, rodent and insect outbreaks, and nutrient run-off spurred by storm events (Yang et al. 2008). Some resource pulses are predictable on a temporal scale (spring green-up of leafy vegetation, fall salmon migration, 17-cicada cycle). Other resource pulses (masting and storm-runoff) arrive with less periodicity, requiring individuals to adapt to unpredictable resource conditions.

Animals that experience resource pulses must adapt their behaviour to maximize their fitness benefits during a pulse and to minimize costs during the intermittent periods of food shortage. Animals adapt to these fluctuations in resources in many ways; they may increase body fat stores, migrate to areas of resource abundance, reduce metabolic demands (torpor), or store food items in times of abundance for use in times of shortage (Smith and Reichman 1984). In many birds and mammals, food hoarding is a common strategy to survive periods of food shortage (see Smith and Reichman 1984 for a review).

Evolution of hoarding strategies

Andersson and Krebs (1987) suggest that hoarding behaviours evolve when the caching individual is more likely than any other to recover that cached food item. Hoarding behaviours can be broadly classified into two categories: scatter-hoarding and larder-hoarding (Smith and Reichman 1984, Vander Wall 1990, Hurly and Lourie 1997). A larder-hoard is a single cache of many food items. In contrast, scatter-hoards are multiple caches of individual (or few) food items. Larder hoarding is the predominant caching strategy of rodents (Vander Wall 1990).

There are many benefits to investing in a larder-hoard. A central hoard allows the owner to minimize energy expenditure during harsh foraging conditions, because very little search effort is required for feeding (Vander Wall 1990). Conditions specific to larder hoards may also increase storage time of food items, allowing the owner to extend the life of the cache through periods of food shortage (Vander Wall 1990). For example, the midden (cache site) of a red squirrel provides moist, cool conditions that prevent cones from opening, maintaining seeds within the cone where squirrels can easily access them throughout the winter (Hurly and Lourie 1997). However, larder hoards can be costly to maintain; they are often conspicuous and the hoarder must have the ability to defend their cache from potential food competitors (Vander Wall 1990, Vander Wall and Jenkins 2003).

Numerous studies have demonstrated that cache pilferage plays a significant role in the spatial distribution of cache sites, such that individuals space caches further apart when they perceive high pilfering risk (Clarkson et al. 1986, Stapanian and Smith 1984, Clarke and Kramer 1994, Dally et al. 2006). Scatter-hoarding strategies are believed to have evolved in species that are unable to defend a larder hoard and experience a high degree of cache pilferage from food competitors (Andersson and Krebs 1978, Vander Wall 1990, Vander Wall and Jenkins 2003, Dally et al. 2006). Cache pilferage is estimated to account for 2-30% of cache losses in long-term hoarders (Vander Wall and Jenkins 2003), suggesting that cache pilferage plays an important role in the dynamics of food storage and recovery.

KLEPTOBIOTIC INTERACTIONS AND CACHE PILFERAGE

Kleptobiotic interactions are a suite of behaviours that involve individuals directly or indirectly competing for food through disputes with the food owner (Vollrath 1984). These behaviours include piracy (acquisition of food by force), pilfering (acquisition of food by stealth), and peculation (acquisition of food by disguise; Vollrath 1984). Kleptoparasitism is another term that has been used to describe this suite of behaviours. This term generally implies an interspecific interaction between a coevolved host and parasite (Vollrath 1984, Iyengar 2008).

Theft is ubiquitous throughout the animal kingdom and is one of the most common forms of exploitation in animals (Iyengar 2008). Kleptobiotic interactions are predicted to evolve under conditions where a) there is a high host concentration, b) food is available for theft in large quantities, c) the food items are high in quality, d) the food supply is temporally predictable, e) the food is detectable in the ambient environment, f) there is an overall food shortage (Brockmann and Barnard 1979, Barnard 1984). Kleptobiotic interactions have been documented in at least 17 taxonomic groups including birds, mammals, arthropods and molluscs (Iyengar 2008).

Kleptoparasitism has been documented most extensively in birds. Brockmann and Bernard (1979) provide an extensive review of documented kleptoparasitic behaviour between birds. Food pilfering occurs most often in species that live in close association and high density, such as colonial sea birds on small islands (Brockmann and Barnard 1979). Kleptoparasitism is also much more common in predatory and opportunistic bird species, such as gulls and corvids (Brockmann and Barnard 1979).

Arthropods are the second most commonly studied group of kleptoparasites. Food stealing is common in flies, spiders, bees, and mites (Vollrath 1984, Sivinksi et al. 1999, Iyengar 2008). Kleptoparasitism has also been documented in crabs, amphipods, echinoderms, and molluscs (Iyengar 2008). Fish have been observed in kleptoparasitic interactions, although documentation is rare (Dominey and Snyder 1988, Hamilton and Dill 2003, Iyengar 2008). Kleptoparasitism has not been reported in toads, frogs, snakes or salamanders; the fast, catch-and-swallow feeding tactics of these species likely prohibit food stealing behaviour (Iyengar 2008).

Several mammals have been documented to steal food (see Table 1). Food hoarding is a common characteristic among mammals who engage in food stealing. A conspicuous cache of high density and high quality food items creates an ideal situation for pilfering behaviours to arise (Brockmann and Barnard 1979, Barnard 1984). Thus, it is unsurprising that pilfering in mammals is common among food-hoarding animals. Rodents are the most common mammals that engage in pilfering behaviour (Vander Wall 1990, Vander Wall and Jenkins 2003). Pilfering behaviour has been studied in rodents primarily by using artificial food caches (Thompson and Thompson 1980, Kraus 1983, Riceoxley 1993, Tamura et al. 1999, Vander Wall 2000, Vander Wall and Jenkins 2003, Dally et al. 2006, Vander Wall et al. 2006). Vander Wall and Jenkins (2003) estimate losses from pilferage for long-term hoarding animals to be between 2-30% a day.

The majority of studies documenting pilfering behaviour in rodents have focused on cache recovery and spatial distribution of scatter-hoarded caches (Vander Wall and Jenkins 2003, Dally et al. 2006). Pilfering is expected to be low among larder-hoarders, since larder-hoarders should be able to effectively defend their cache from pilferage (Vander Wall and Jenkins 2003, Dally et al. 2006). There are very few studies of pilfering in larder-hoarding animals (McKechnie et al. 1994, Devenport et al. 2000, Leaver and Daly 2001, Edelman et al. 2005, Gerhardt 2005). Most of these studies suggest the incidence of pilferage from larder-hoards is low (McKechnie et al. 1994, Devenport et al. 2000, Edelman et al. 2005); however Gerhardt (2005) suggests pilferage loss in larder-hoarding red squirrels to be as high as 25% of the cache.

Pilfering is an alternative foraging strategy that may provide certain individuals an alternative technique for acquiring food resources (Broom and Ruxton 1998, Vander Wall and Jenkins 2003, Dally et al. 2006, Iyengar 2008). Pilfering is likely a costly behaviour in larder-hoarding species. The food thief is exposed to several costs such as increased predation risk, increased conspecific aggression, and potential loss from their own cache to other pilferers. The benefit of obtaining additional food resources must outweigh the costs of this alternative foraging behaviour, if the behaviour is to be maintained in the population (Broom and Ruxton 1998). The low occurrence of pilfering among larder-hoarders suggests that generally the costs of pilferage outweigh the benefit for individual pilferers, and the behaviour should occur rarely in larder-hoarding individuals.

Red squirrels are an ideal species to examine hoarding and pilfering behaviours, because their caches are conspicuous, they are highly territorial, and individuals can be easily trapped and monitored. Edelman et al. (2005) reported low incidence of pilfering in Mount Graham red squirrels (*Tamiasciurus hudsonicus* grahamensis) in Arizona, USA.

However, Gerhardt (2005) found high rates of pilferage (26%) in a study of red squirrels in Vermont, USA. The purpose of this project was to investigate pilfering and larder-hoarding in red squirrels in Kluane, Yukon, Canada. The objectives of this thesis were to 1) quantify resource availability and cache size of individuals in the study area, 2) quantify the relationship between the food cache and survival, 3) estimate the amount of pilfering occurring among individuals in a population, 4) to identify distinguishing characteristics of food pilferers (age, sex, winter cache size), 5) compare overall rates of pilfering between two populations that differ in both quantity and availability of resources, and 6) compare pilfering rates in Kluane, YT to those published for red squirrels in other parts of their extensive range. These objectives were achieved by estimating fall cone availability and fall cache size through survey and quadrat sampling, a mark-recapture study of cached cones to document pilfering events, and an experimental removal of midden owners to observe pilfering behaviour.

STUDY SYSTEM

RED SQUIRRELS

North American red squirrels are a small, arboreal species that range across Canada's forests and extend down into much of the USA (Steele 1998). Red squirrels are highly territorial, and defend non-overlapping territories year-round (Smith 1968, Gurnell 1984). Red squirrel territories usually contain one or more larder-caches (middens), where squirrels cache coniferous seed. Middens are large, conspicuous piles of cone bracts, which have formed over time as the squirrels consume seeds from coniferous cones (Gurnell 1984). Red squirrels rely on their larder-hoarded caches of coniferous cones for over-winter survival (Smith 1968). Red squirrels are known to vary in the degree of scatter-hoarding versus larder-hoarding behaviour throughout their range (Smith and Reichman 1984, Dempsey and Keppie 1993, Hurly and Robertson 1990, Hurly and Lourie 1997).

Female red squirrels usually give birth between March and June. Juveniles emerge from the nest approximately 50 days later, and are weaned by 70 days (Humphries and Boutin 1996, Boutin et al. 1993). Juveniles must obtain a territory with a midden in order to survive the winter (Smith 1968, Boutin et al. 1993, Berteaux and Boutin 2000). Some red squirrel mothers will bequeath part or all of their territory to offspring to improve their juvenile's chance of survival (Boutin and Schweiger 1988, Berteaux and Boutin 2000). Predation of red squirrels is primarily by northern goshawk (*Accipiter gentilis*), lynx (*Lynx canadensis*), great-horned owl (*Bubo virginianus*), and coyote (*Canis lantrans*) (Stuart-Smith and Boutin 1995).

KLUANE RED SQUIRREL PROJECT

The Kluane Red Squirrel Project is an ongoing collaborative research initiative investigating the ecology, evolution and energetics of red squirrels. The project is located at 61°N, 138°W, near Kluane Lake, Yukon. Populations here have been monitored extensively since 1987. All individuals within the study populations are known; individuals are marked at birth. Each squirrel in the population receives unique ear-tags, as well as coloured markers for identification at a distance. Using behavioural observations and live-trapping, all individuals can be followed from birth until death.

Red squirrels in Kluane are dependant on the only source of coniferous seed, which is the white spruce (*Picea glauca*) (Dale et al. 2001, Garbutt et al. 2006). The cones are available to the squirrels for a short period (late summer to early fall). Squirrels must cache the spruce cones in their middens within a few weeks of the cones maturing; un-cached cones will open and disperse seed in early fall, making the seed unavailable to the squirrels. White spruce is a masting species, which produces variable seed crops from year to year (LaMontagne and Boutin 2007). Some years trees produce no or very few, cones. Approximately every 5-7 years, a masting event will occur, and most trees will produce hundreds of cones (LaMontagne and Boutin 2007). This boom-bust cycle creates a variable selective environment (McAdam and Boutin 2003a, McAdam and Boutin 2003b), which may generate a mosaic of behavioural adaptations to both low and high food conditions.

THESIS CHAPTERS

This thesis is comprised of two data chapters. Chapter II, “Interspecific cache pilferage by red squirrels (Tamiasciurus hudsonicus) in Kluane, Yukon”, covers the primary objectives of this thesis by examining individual propensity for cache pilferage and quantifying pilfering rates in this region. The results in this chapter provide evidence that squirrels in the region are capable of cache pilferage, but the behaviour is rare when individuals can defend their cache. Chapter III is a brief examination of the role of cone availability and fall cache size in the over-winter survival of red squirrels in the Kluane region. It is entitled “The influence of food hoarded on survival in North American red squirrels”. The results of this chapter suggest age and fall cache size were the strongest predictors of over-winter survival in red squirrels between 2008 and 2009. Together these chapters suggest individuals in this region depend on a sizable food cache for over-winter survival and strongly limit the opportunity for cache pilferage, resulting in low rates of overall cache pilferage in the population.

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Table 1-1. A list of food-stealing mammals derived from Vander Wall (1990), Vander Wall and Jenkins (2003), Dally et al. (2005), Iyengar (2008), and Web of Science (search terms kleptoparasitism, pilferage, pilfering, theft, and scrounger)

Common Name	***Scientific Name***	**Reference**
Chipmunks		
Eastern Chipmunk	*Tamias striatus*	Clarke and Kramer 1994
Yellow Pine Chipmunk	*Tamias amoenus*	Vander Wall 2000, Vander Wall et al. 2006, Vander Wall 1991
Foxes		
Red Fox	*Vulpes vulpes*	Henry 1986
Arctic Fox	*Alopex lagopus*	Careau et al. 2007
Hyenas	*Crocuta crocuta*	Caraco and Wolf 1975, Creel and Creel 1996, Gorman et al. 1998
Kangaroo Rats		
Merriam's kangaroo rats	*Dipodomys merriami*	Daly et al. 1992, Longland and Clements 1995, Leaver and Daly 2001, Preston and Jacobs 2001, Leaver 2004, Murray et al. 2006
Pocket Mice	*Chaetopipus spp.*	Leaver and Daly 2001
Minke whales	*Balaenoptera acutorostrata*	Hoelzel et al. 1989
Pikas	*Ochotona princeps*	McKechnie et al. 1994
Sea otters	*Enhydra lutris*	Riedman and Estes 1988
Squirrels		
Eurasian Red Squirrel	*Sciurus vulgaris*	Riceoxley 1993
Fox Squirrel	*Sciurus niger*	Stapanian and Smith 1984
Gray Squirrels	*Sciurus carolinensis*	Thompson 1980, Kraus 1983, Leaver et al. 2007, Hopewell et al. 2008, Schmidt and Ostfeld 2008, Thompson and Thompson 1980, Steele et al. 2008
Japanese Squirrel	*Sciurus lis*	Tamura et al. 1999
North American Red Squirrels	*Tamiasciurus hudsonicus*	Gerhardt 2005, Edelman et al. 2005
Southern Flying Squirrels	*Glaucomys volans*	Winterrowd and Weigl 2006

CHAPTER II

INTRASPECIFIC CACHE PILFERAGE BY RED SQUIRRELS (*TAMIASCIURUS HUDSONICUS*) IN KLUANE, YUKON

INTRODUCTION

Food pilfering has been observed in a variety of birds and mammals (Brockmann and Barnard 1979, Iyengar 2001, Vander Wall and Jenkins 2003, Dally et al. 2006, Iyengar 2008,). Pilfering (when one individual takes food that has been procured by another), is an exploitative behaviour that occurs both inter- and intra-specifically. Among mammals, stealing and caching food items is commonly reported in animals that store food for later consumption (Leaver and Daly 2001, Leaver et al. 2007, Vander Wall et al. 2006).

Food-hoarding is commonly seen in animals that must survive periods of food shortage (Vander Wall 1990). Individuals should hoard food in a way that maximizes recovery for the hoarder, and minimizes recovery by food competitors (Andersson and Krebs 1978). Mammals vary greatly in their approach to food hoarding; some may hoard most of their food items in a large, central cache (larder-hoarding), and others may hoard a few food items in a number of small, dispersed caches (scatter-hoarding; Vander Wall 1990). Larder-caches are thought to be the ancestral form of food-caching behaviour in rodents (Vander Wall 1990). The larder-cache minimizes both the time spent foraging during periods of food shortage, and the time spent managing the food cache, when compared to scatter-hoarded caches (Vander Wall 1990). However, conspicuous, high-density larder-hoards are susceptible to pilferage by food competitors. Food-hoarders may minimize pilferage in two ways; they may increase the dispersion of their food caches (scatter-hoard), or they can aggressively defend their caches against intrusions (Vander Wall and Jenkins 2003). Thus theory on caching behaviour predicts that larder-hoarding should be observed in animals that can effectively defend their caches from pilferage, while scatter-hoarding is predicted in animals who can not exclude competitors from a central cache site (Andersson and Krebs 1978, Vander Wall 1990, Vander Wall and Jenkins 2003).

Several studies have attempted to estimate the occurrence of pilfering among food hoarders using artificial food caches. Losses from artificial caches have been estimated to be between 2 and 30% per day (Vander Wall and Jenkins 2003). The majority of these studies have focused on rodents and birds who scatter-hoard (Thompson and Thompson 1980, Kraus 1983, Stapanian and Smith 1984, Riceoxley 1993, Tamura et al. 1999, Vander Wall 2000). Fewer studies have examined pilferage by larder-hoarders (McKechnie et al. 1994, Devenport et al. 2000, Leaver and Daly 2001, Edelman et al. 2005, Gerhardt 2005), and only two have measured pilferage under natural conditions (McKechnie et al. 1994, Gerhardt 2005). Thus, despite extensive observations of pilfering behaviour and studies of artificial cache depletion, the factors which influence pilfering behaviour under natural conditions remain unclear.

Red squirrels (*Tamiasciurus hudsonicus*) are an ideal species to investigate pilfering behaviour in a food-caching mammal. Red squirrels are small, arboreal, food-hoarding rodents who extend throughout the coniferous forests of North America (Smith 1981, Steele 1998). Red squirrels defend non-overlapping territories year-round, which contain larder-caches of conifer cones (middens; Smith 1981, Gurnell 1984) that are conspicuous and easy to locate. The primary food source of red squirrels (coniferous cones) is quantifiable in the fall, and squirrels are also easily trapped, marked and monitored. Squirrels have a few interspecific competitors for cones while the cones remain on the tree (crossbills and nuthatches); however, once the cones have been cached within the midden they are only removed by red squirrels (Smith 1981, Gerhardt 2005).

Because red squirrels experience prolonged periods of food shortage throughout their range, but are highly territorial, and can aggressively defend a larder-hoard (Smith 1968a, Rusch and Reeder 1978, Gurnell 1984), squirrels should experience low cache pilferage. However, previous studies of pilfering behaviour in red squirrels have been equivocal. Edelman et al. (2005) studied pilfering in Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) using cone-baited stations with camera traps at middens occupied by red squirrels (n=9).

Their results suggest that pilfering from occupied middens is rare; of all the individuals observed by midden camera traps, the mean number of non-resident red squirrels captured was 0.3 ± 0.2. In contrast, Gerhardt (2005) found that pilfering by red squirrels under natural conditions was remarkably common, with 97% of individuals (n=29) engaging in the behaviour. Pilfering by conspecifics accounted for 25% of cache-losses in his study area (Vermont, USA). This marked deviation from the expectations of pilfering behaviour in red squirrels merits further investigation.

Red squirrels should only pilfer when the energetic benefit of the pilfered item is greater than the cost of obtaining that item. Individuals who pilfer food can increase their cache size, which may induce other benefits such as an increased chance of survival in periods of food shortage, or an increase in food available to invest in energy for reproduction (LaMontagne 2007). However there are several potential costs associated with pilfering. Pilfering individuals leave their own caches undefended, which can make their cache susceptible to pilferage by conspecifics. In addition, individuals may be more susceptible to predation as they foray outside of their familiar territory to pilfer (Brown 1988, Brown 1992, Brown et al. 1992). Pilfering individuals may also experience more conspecific aggression from their neighbours (Vollrath 1984). Since larder-hoarding red squirrels are dependent on their winter food cache for over-winter survival (Smith 1967a, Steele 1998, LaMontagne 2007, and see

CHIII), and strongly defend their caches through territorial calls and chases (Stuart-Smith and Boutin 1995), pilfering from larder-hoarding neighbours may be challenging; requiring stealth and cunning for success. Thus pilfering is a potentially costly behaviour for red squirrels, which should only occur when the pilfered item is highly valued and has potential fitness benefits.

Brockmann and Barnard (1979) predicted several ecological factors which could influence the occurrence of pilfering in a population: a high concentration of hosts, large quantities of high-quality food available, predictable food supply, a conspicuous food source, and an overall food shortage in the population. Several of these conditions are commonly observed in most populations of larder-hoarding red squirrels (Rusch and Reeder 1978, Smith 1981, Gurnell 1984); food resources are seasonally and spatially predictable, concentrated in detectable locations (middens), and individual cones are of high energetic value (see Smith 1967). In populations where intraspecific theft occurs there should be more pilfering when the overall quantity of coniferous cones available in the environment is low, and it is difficult to obtain an adequate food cache though cone harvesting alone. When cones are abundant, the benefit to cost ratio of pilfering is lower and therefore less pilfering should occur. The population density of red squirrels may also influence the overall amount of pilfering in the population; at high density per-capita food resources are lower, and therefore pilfering should be higher than in a similar population but with low population density. The amount of cache pilfering occurring in a population should also depend on the level of cache defence. The midden is a concentrated, conspicuous source of high quality food, and would be attractive to thieves. However, red squirrels must expend a lot of energy to build a cache for over-winter survival (Humphries and Fletcher, unpublished data), and therefore should strongly defend their investment from cache from pilferage. The high intensity of defence by territorial red squirrels likely decreases the opportunities for cache pilferage in larder-hoarders. Thus the degree of food shortage during winter likely affects both the number of thieves present and the opportunities for cache pilferage in populations of red squirrels.

Within a population, individual variation in pilfering behaviour can be predicted based on a variety of factors which relate to an individual's ability to obtain and defend a food cache. Age and body condition, sex, cache size, and neighbouring squirrels may all influence both an individual's defence of their own cache from pilferage and their propensity to steal from others. Younger individuals and those who are in poorer body condition may be less effective at cache defence due to inexperience or physical limitations, and thus may be predicted to experience more theft. Since juvenile squirrels are both inexperienced foragers, and have smaller territories (LaMontagne 2007) with potentially less food, they should also be more likely to pilfer than adults. Alternatively, older or bolder individuals may be more likely to pilfer, because experience allows them to minimize their costs of cache pilferage (predation risk, losses from their own middens, interactions with neighbours). The reproductive activities of red squirrels may also lead to differences in both cache defence and pilfering by males and females. During the mating season, males leave their territories undefended while they chase females for breeding opportunities (Lane et al. 2009), and leave their caches susceptible to pilferage. Since females also relax territorial defence during their mating chase (Lane et al. 2008), individuals may also have more opportunity to pilfer during the breeding season. The cone caches of females may also be more susceptible to pilferage later in spring, during the ~40 days that offspring remain in the natal nest (Humphries and Boutin 2000). Thus breeding animals, especially females, may be more susceptible to cache pilferage than non-breeders, and males may be more likely to pilfer from females who are mating or rearing young. Winter cache size is also likely an important factor to explain variation in pilfering behaviour among individuals in a population. Red squirrels require a large cache of coniferous cones to survive winter (Smith 1968b, LaMontagne 2007). Pilfering may be an alternative foraging strategy for some individuals when there are few cones on the landscape, but neighbours have large caches of stored cones nearby. Thus higher cache pilferage is predicted when individuals have smaller winter food caches than their neighbours. Finally, the density of neighbouring squirrels may influence the amount of pilfering from an individual cache. An individual’s food cache may be more susceptible to pilfering if they have a high density of neighbouring squirrels, because there are more individuals to defend the cache against. So the amount of pilfering occurring within a population may depend on a variety of proximate factors that relate both to individuals' abilities to exclude potential thieves and the number of thieves in the population, which ultimately leads to variation in pilfering behaviour within the red squirrel species.

The purpose of this study was to use both experimental and observational approaches to identify the proximate mechanisms that lead to variation in pilfering behaviour among individuals and between populations of red squirrels. The objectives of this study were: 1) to estimate individual levels of pilfering within a population of red squirrels, 2) to examine potential variation in individual pilfering rates related to age, sex, neighbour density and winter food cache size, and (3) to compare pilfering rates in a natural population of red squirrels, to a manipulated population that has received experimental food addition since 2004.

This study took place in Kluane YT, using a subset of research grids established by the Kluane Red Squirrel Project (see Berteaux and Boutin 2000, Humphries and Boutin 2000). I expected juveniles, males, and those with smaller caches to pilfer most often, and predicted higher rates of cache pilferage by squirrels in the un-manipulated population, compared to squirrels who were receiving experimental food additions. I used an experimental study where I removed the midden owner, to examine the potential for pilfering by individuals in this region. To estimate the natural rate of pilfering among Kluane red squirrels, I used a mark-recapture study of marked spruce cones.

METHODS

STUDY SITE

I studied pilfering behaviour of red squirrels in Kluane, Yukon (61°N, 138°W) between September 2008 and June 2009. This population has been monitored extensively since 1987. A detailed description of the study site and project protocols can be found elsewhere (Berteaux and Boutin 2000, Humphries and Boutin 2000). All individuals in the study areas are individually marked at birth, and given uniquely numbered ear tags with coloured markings for visual identification, allowing for complete enumeration of the population. Breeding condition of adults is assessed during bi-weekly live-trapping.

This study took place on two study grids, which are staked at 30m intervals and marked with flagging tape. The habitat at both sites is open boreal forest dominated by white spruce (Berteaux and Boutin 2000, Humphries and Boutin 2000). One study site is supplemented with peanut butter throughout the winter months, as part of a larger ongoing study of population-level effects of food addition. Density on this site (food add), is 4.4 squirrels per hectare. The second site (control) is an un-manipulated site with 1.9 squirrels per hectare, and experiences natural annual fluctuations in food-availability. Cone resources in this region were at low levels during this study. The most recent mast-seeding event occurred in 2005 (LaMontagne and Boutin 2007) when 65.5 cones per tree were produced. In all years since then most trees have produced few cones: 1.2 cones per tree in 2006, 7.1 in 2007, and 2.2 in 2008 (Boutin and McAdam, unpublished data).

TERRITORY MAPPING

The midden locations of all individuals in the study area were determined through a bi-annual population census of midden occupancy, as well as periodic live trapping. Territories were mapped by obtaining behavioural observations of the focal squirrel. Individuals were located by sight or sound and followed until they disappeared from view (Price et al. 1986, Larsen and Boutin 1994). The location of all territorial behaviours (eating, vocalizing, caching) was recorded by an observer. I obtained an average of 26 observations per squirrel (minimum 9, maximum 58) between June and September 2008 for 71 individuals. For juveniles I obtained fewer observations because they settled territories late in the year; an average of 16 observations was obtained per squirrel (minimum 8, maximum 29). I generated territory estimates using 95% minimum convex polygons using Home Range Tools for ArcGIS (Ontario Ministry of Natural Resources, Thunder Bay, Canada, 2002). In September 2008 there were 66 squirrels with primary middens in the study areas; 19 males, 13 females, and 3 juveniles on the control grid (n=35), and 15 males, 12 females, and 6 juveniles on the food-add grid (n=33).

I used data from trapping records and the spring midden census of the Kluane Red Squirrel Project to determine overwinter survival of individuals. During this census all known middens are trapped and monitored for red squirrel activity, and individual owners are identified using behavioural cues such as rattle calls, barking, and frequent trapping at the site. Squirrels no longer present in the population after May 1st 2009 were considered deceased.

FALL CACHE SIZE

To examine the influence of food resources on pilfering behaviour, I estimated the amount of food hoarded by individuals following the caching season in fall 2008. The cache size in the primary midden of each individual in the study area was estimated using quadrat sampling. The midden was separated into 4 quadrants by marking an X through the centre of the midden. Four 0.6 X 0.6 m quadrats were placed within each quadrant at equal spacing. All closed spruce cones inside the quadrat, to a maximum depth of 20 cm, were counted. Cones of the year (new) were distinguished from cones from previous years (old) based on colouration; new cones were purple-green while old cones were brown. The length and width of the midden were measured and used to estimate the area of the midden (assuming an elliptical midden shape). The number of cones found in each quadrat was averaged and multiplied by the estimated area of the midden to estimate total cache size.

OWNER REMOVAL EXPERIMENT

I conducted an experimental manipulation of midden owners to assess the propensity of red squirrels in the study area to pilfer when the owner was absent. The experiment was conducted in September of 2008, immediately following the fall caching period. Randomly selected red squirrels (n=44) were live-trapped following Kluane Red Squirrel Project protocols, using Tomahawk traps and peanut butter as bait. Once trapped, the midden owner was transferred to a modified tool box, which keeps squirrels calm and quiet while in captivity. The captured squirrel was moved approximately 20-30 m away from the midden for the duration of the trial. An observer sat within 5 m of the midden and monitored it for any pilfering activity. The observer recorded the identity of any pilferers, the number of intrusions, the number of items taken, and any other behaviour during the intrusion. Following a two-hour observation period, the captive squirrel was released at the site of capture.

MARK-RECAPTURE PIN STUDY

I conducted a mark-recapture study to estimate the natural rates of pilfering activity by red squirrels in the study areas. I used 26 mm nickel-plated dress-making pins to mark individual spruce cones. Pins were inserted inside the rachis of the cone, making them virtually undetectable to the squirrel. Pins were painted with a unique colour combination along the length of each pin, using Tremclad metal primer and metal paint. Each squirrel in the study area was assigned a unique colour of pin (Appendix 1).

Cones were marked during the month of September, when cone caching was nearly complete. The two study sites differed in the number of available spruce cones on each midden; therefore 100 cones per primary midden were marked in the food-add study area, and 200 cones per midden were marked in the control area. Only closed cones within 10 cm of the midden surface were marked. Only new cones were marked, unless there were insufficient new cones, in which case old cones were also marked. In total I marked 9900 spruce cones on 66 primary middens.

From May-June 2009 I returned to each primary midden to search for pins. Middens were searched using Garrett Ace 250 metal detectors with a Sniper-coil attachment. To search a midden for pins, first the entire midden was scanned using a metal detector and flags were used to mark detected pin locations (detected locations). When pins were detected, the top layer of cone bracts (usually from 5-10cm deep) within ~0.5 m of detected locations was scooped into a bucket. Pins were recovered from the bucket by waving the detector over smaller piles of bracts (a handful). Before returning the searched bracts to the midden, the midden was scanned with a detector a second time. This protocol was repeated on primary middens three times, by at least 2 separate observers. Secondary and tertiary middens were also searched. To search for pins off of the middens, I scanned the ground using the metal detector along 80 random 30 m transect lines, covering an area of 4800 m^2 within each of the study areas.

I recorded the colour and location of any pins recovered. I used territory information, spring census data, and the pin colour key to distinguish the midden of origin for each pin. Any foreign coloured pin found on a midden was considered a pilfering event. Pins recovered on the middens of deceased squirrels were excluded from the data.

STATISTICAL METHODS

I used independent T-tests in SPSS 16.0 to examine differences in number of cones cached between the sexes and age classes, as well as differences in age between pilfering squirrels and non pilfering squirrels. I used Levene’s Test for Equality of Variances to test for homogeneity of variance in the data, and used Independent T-tests Assuming Unequal Variances when the assumptions were not met. I used a General Linear Univariate model to analyze differences in food cache size between pilfering and non-pilfering squirrels to account for age, sex, and site effects. Cache size data were natural log transformed to meet with assumptions of normality. I compared over-winter survival and sex differences of pilfering and non-pilfering individuals using Pearson Chi Square analysis. For all tests an alpha value of 0.05 was used.

To calculate pilfering rates I used a modified version of the Lincon-Peterson index, with a correction factor for the proportion of cones marked and the proportion of markers (pins) recovered, which was developed by Gerhardt (2005). The estimated number of cones stolen by each squirrel was calculated using the equation:

$$\text{Stolen cones} = (C*P_s)/\ (P_m*P_r)$$

Where C is the estimated number of cones cached in fall 2008, P_s is the number of stolen markers recovered on the owner's midden, P_m is the number of cones originally marked on that midden, and P_r is the proportion of cones marked in 2008 that were recovered in 2009 (X=0.61 ± 0.02, range 0.22-0.92). The percentage of cones gained by stealing was calculated by dividing the estimated number of cones stolen by the estimated total fall cache size.

RESULTS

FALL CACHE SIZE

In fall of 2008, squirrels had an average (±SD) of 6938.3 ± 6365.1 spruce cones cached in their primary middens. Squirrels had an average of 4420.5 ± 5140.1 spruce cones remaining in their middens from the fall of 2007. The average number of new cones cached differed between the two study sites (Table 1); squirrels on the control site cached more new cones than squirrels on the food-add site. On average squirrels on the control site also tended to have more total cones cached (new and old) than squirrels on the food-add site (Table 1). However, total cache size was highly variable on both sites (cache size on the control site ranged from 171.8 to 25904.7 cones, while cache size on the food-add site ranged from 27.1 to 29484.7 cones) and therefore there was no statistical difference between the overall numbers of cones cached per individual between the two sites (Table 1).

In fall 2008 males had significantly more cones in their middens than females ($T_{66}=2.836$, $p=0.006$; Fig 2-1). Juvenile red squirrels who had settled a territory also had significantly fewer cones than adults ($T_{66}=-4.401$, $p<0.001$; Fig 2-2).

OWNER REMOVAL EXPERIMENT

During the 44 removal experiments I observed 31 cases (70% of trials) of non-territory owners intruding on the focal territory. Of these invasions, squirrels removed food items from the focal midden 74% of the time. Food items taken during the removal experiment included mushrooms, new cones and old cones. On average, squirrels invaded the focal territory after 70.8 ± 33.7 (SD) minutes (minimum 4, maximum 120). Squirrels generally behaved stealthily; they moved slowly and cautiously, with no vocalization. Intruding squirrels occasionally fed on the midden, however usually only after stealing several food items; the average ratio of food items stolen to food items eaten was 8.4 ± 7.7 (SD).

Males and females were equally likely to appear during the experiment (X^2_1=0.247, p=0.619). Squirrels who pilfered during the owner removal tended to be younger than squirrels who did not pilfer (T_{72}=1.940, p=0.056; Fig. 2-3). Squirrels who pilfered during the removal experiment had an average of 4349.4 ± 1375.3 (SE) cones cached, while squirrels who did not pilfer had an average of 6962.2 ± 855.9 (SE) cones cached. There was a significant difference in the amount of food cached between squirrels who pilfered during the experiment and those squirrels who did not pilfer after accounting for site, age, and sex ($F_{1,69}$=4.843, p=0.031). Squirrels who pilfered during the experiment were significantly less likely to survive the winter than squirrels who did not pilfer (X^2_1=4.820, p=0.028).

MARK-RECAPTURE PIN STUDY

In total I recovered 6237 (63%) pins on 67 middens; 4407 (67%) in the control study area and 1830 (55%) in the food-add area. All pins that were recovered were on primary middens. In one case I recovered pins on a midden that had not been marked the previous fall. Most pins were recovered from the discarded rachis of cones; others were found lying in the bracts, few remained inside cached cones. I was able to identify the owner of all pins found on middens of living squirrels.

Pins were rarely visible to the naked eye. The majority of pins recovered were found using the metal detectors. The number of pins recovered (for living squirrels) was generally consistent between middens

(61.3 ± 13.9% SD). There was no significant relationship between the number of pins recovered and the area (m^2) of the midden (R^2=0.051 ± 0.132, p=0.115), or pin recovery and the number of cones cached in the midden in fall 2008 (R^2=0.002 ± 0.136, p=0.787), thus pin recovery was not biased by midden area or cache size.

From a pilot experiment testing the recovery of intentionally placed pins, it was known detectors failed to detect pins approximately 1/3 of the time (Appendix 2). The metal detectors were effective in recovering pins when the detector was within approximately 5 cm of the pin. The detectors were unable to detect pins below this depth, unless bracts were removed from the area. All pins recovered were found on a midden, despite extensive searches of the surrounding areas. Thus, unrecovered pins from this experiment likely remain in the middens.

Seven (14%) of 51 squirrels that survived over-winter engaged in pilfering behaviour between October 2008 and May 2009; 2 squirrels in the control study area, and 5 in the food-add area. All pilfering individuals during the mark-recapture pin study were adults; 3 were male and 5 were female. There was no significant difference between the number of cones cached in 2008 by squirrels who pilfered and squirrels who did not pilfer ($F_{1,67}$=1.568 p= 0.215). Pilfered cones were always from adjacent middens. In the food-add study site, 18% of pilfering events were from middens where the owner died at some point during the winter. In the control study area 67% of detected pilfering events were from a single unoccupied midden where the owner was deceased. I found no evidence of reciprocal cache pilferage (see Vander Wall and Jenkins 2003). There was no significant difference in the amount of cones stolen between the 2 study sites (t_5=-0.172, p=0.870). Pilfering squirrels gained an estimated average of 169.4 ± 68.9 (SE; minimum 19.4, maximum 536.0) cones by stealing. On average, this represented approximately 2.1 ± 0.5% (SE) of their total cache. However, cones obtained by pilfering represented only 0.3% of the total amount of cones cached by squirrels in the study areas in 2008; 0.1% on the control site and 0.7% on the food-addition site.

Eight (16%) squirrels who survived over-winter lost cones to intraspecific pilfering; 2 in the control study area and 6 in the food-add site. 5 of those squirrels were female, and 3 were male. These squirrels lost an average of 70.3 ± 20.9 (SE) cones to pilfering or approximately 2.1± 0.8% of their total cache. There was no significant difference in the amount of cones stolen from squirrels between the study sites (T_8=-0.891, p=0.399). Of the 8 juveniles who survived over-winter, 2 experienced cache pilferage. All other squirrels who experienced pilfering were breeding adults.

DISCUSSION

Pilfering in Kluane red squirrels occurred at a much lower rate than has been previously been reported in red squirrels (Gerhardt 2005), or other long term hoarding animals (see Vander Wall and Jenkins 2003).

Larder-hoarding red squirrels are predicted to experience low cache pilferage because they are highly territorial and can aggressively defend their cache from intrusions (Smith and Reichman 1984; Vander Wall 1990; Vander Wall and Jenkins 2003; Dally et al. 2006). The low rates of cache pilferage in the study areas support these theoretical predictions, but differ greatly from the high intraspecific pilfering rates reported by Gerhardt (2005).

Results from the experimental removal of midden owners demonstrate that individual red squirrels in this region are capable of cache pilferage when given the opportunity. There was no evidence for differences in pilfering behaviour between males and females in this study; both sexes were equally likely to appear during the owner removal experiment. These results are supported by other studies of pilfering behaviour which also found no significant differences between sexes of pilfering individuals (McKechnie et al. 1994; Gerhardt 2005). Squirrels who pilfered during the experiment were significantly younger than squirrels who did not pilfer, supporting the prediction that younger, more inexperienced individuals have a greater propensity towards cache pilferage. Gerhardt (2005) found there was no difference in pilfering behaviour between juveniles and adults. However 62% (18) of individuals included in the Vermont study were juveniles, 24% (7) were of unknown age and only 14% (4) were known adults, thus the ability to detect an age effect may have been limited by the sample size of adult squirrels.

Individuals that pilfered during a removal had less food cached for the winter than squirrels that did not pilfer, and were also significantly less likely to survive until spring, supporting the predictions that individuals may be more likely to pilfer when they have small or inadequate food caches for over-winter survival. A previous study in this region suggested that red squirrels need a minimum of 7200 spruce cones cached to survive and reproduce the following spring (LaMontagne 2007); 19 of the 23 squirrels who were observed pilfering during removals had less than 7200 cones cached. Thus, this experiment suggests that squirrels who have few or no cone resources for over-winter survival have a greater propensity to attempt cache pilferage from their neighbours. The removal experiment allowed me to manipulate the opportunity for cache pilferage and observe the propensity for pilfering behaviour within a natural population. The experimental results suggest that the propensity to pilfer is primarily driven by age and food limitation in Kluane red squirrels.

During the 8 months of the mark-recapture pin study the natural rate of cache pilferage in Kluane was low. All victims of cache pilferage were squirrels with neighbouring middens; proximity to a pilfering squirrel seems to be best predictor of who gets stolen from. I was unable to analyse site-level differences in natural pilfering rates between the food-manipulated and control sites because of the small number of pilfering squirrels in the study areas during the mark-recapture study (7 individuals). However, for both sites very few cones were lost to pilfering and few individuals who survived over-winter engaged in pilfering behaviour. These results are supported by Edelman at al. (2005) who also found very low occurrence of pilfering among Mt. Graham red squirrels, and McKechnie et al. (1995) who found pilfering from hay piles to be an infrequent behaviour in larder-hoarding pikas. Nonetheless, the natural pilfering rate of 0.3% reported here is considerably less than the 26% rate of cache pilferage reported for the same species in Vermont, USA (Gerhardt 2005).

The overall amount of pilfering occurring in a population depends on both the number of individuals pilfering and the opportunity for cache pilferage. The removal study has demonstrated that individuals in the Kluane region are capable of cache pilferage; however the low rates of natural cache pilferage detected over the course of this study suggests that red squirrels in this region defend their cache aggressively and minimize opportunity for pilferage. During the removal experiment, the midden was undefended by the owner and no vocalizations took place. Despite this, squirrels generally did not arrive at the vacant midden to pilfer until over one hour into the trial; suggesting that neighbours are aware of the territorial vocalizations of the midden owner (Smith 1978), and are waiting for opportunities when they are confident the owner has left the midden undefended before attempting intrusions. McKechnie et al. (2005) only observed pikas pilfering from hay piles when the owner was away from their burrow. Red squirrels who own middens in Kluane rarely leave their territories; except during the reproductive season when males will leave to search out receptive females (Lane et al. 2008, Lane et al. 2009). The removal experiment provided an opportunity for pilfering to individuals who would have normally been immediately driven away from the midden through vocalizations or physical aggression by the owner (Smith 1978, Price et al. 1990, Price 1994).

The opportunity for cache pilferage in this region is likely limited by the strong territorial defence of the central midden by red squirrels. Extended periods of low abundance of food resources, high energy demands during caching, and limited alternative resources during winter, make the larder cache of spruce cones a valuable commodity for red squirrels, which should be strongly defended against intruders. Red squirrels in Kluane require a cache of spruce cones to survive the approximately 8 months of winter food-shortage (Smith 1968, Steel1998, LaMontagne 2007, see Chapter III); during the study, only squirrels who occupied middens in fall 2008 survived to the following spring. White spruce, which comprises 50% to 80% of red squirrel diets (LaMontagne 2007; McAdam and Boutin, unpublished data), is the only source of coniferous seed available to red squirrels in this region. White spruce cones mature in late August and must be cached within a few weeks to prevent seeds from dispersing (Personal observation). Harvesting new cones during this time is the most energetically demanding period for red squirrels, requiring approximately 4 times their basal metabolic rate (Fletcher and Humphries, unpublished data). In years of low food this activity may become even more energetically expensive, because squirrels have to visit more trees with fewer cones per tree (LaMontagne 2007). Clipping and caching cones supersedes both reproduction and lactation, in terms of energy expenditure (Fletcher and Humphries, unpublished data), and therefore represents a substantial energetic investment, which should be strongly defended. In Kluane high territorial defence of the central midden likely excludes most pilfering activity, making the opportunity for cache pilferage rare.

The majority of individuals observed pilfering in this region were juvenile squirrels with small winter caches who did not survive the winter. This suggests that when squirrels are highly dependent on their cache for survival, pilfering is generally an ineffective foraging strategy for overcoming food limitation. There were a small number of squirrels detected pilfering between fall and spring. These squirrels did not differ in any detectable way from an average squirrel in Kluane, and seem to successfully use pilfering in conjunction with normal foraging in the fall to maintain adequate food stores. Ultimately in Kluane pilfering is a rare behaviour that is beneficial to a very small number of squirrels who can augment their own caches with stolen cones. The small amount of cones stolen by these individuals (0.3%) is unlikely to influence population level responses to resource conditions in this region.

From 2008-2009 cache pilferage was much less common in red squirrels in the Kluane region, compared to rates reported for red squirrels in Vermont (Gerhardt 2005). Individuals were seven times less likely to engage in pilfering behaviour, and stole only 0.3% of cones cached, compared to Vermont red squirrels who stole 26% of their food cache. There are several differences between these populations that may explain some of the discrepancy in pilfering rates. Sixty-two percent of the population studied in Vermont were juveniles, compared to only 15% in the study areas. In this study I found younger squirrels were more likely to steal; the greater proportion of individuals pilfering in Vermont compared to populations in the Kluane region could be partially explained by differences in the proportion of juveniles in the population. Density may also play a role in the differences in propensity for individuals to pilfer. Density at the study sites was 1.9 (control) and 4.4 (food-add) squirrels per hectare, while density at the Vermont site was 9.9 squirrels. At high densities intruder pressure at midden sites would increase, potentially making it more difficult to defend a cache. I observed more pilfering individuals and a greater number of cones stolen on the higher density site compared to the low density site, although these results should be interpreted with caution due to the small sample size. An increase in intruder pressure on food caches related to the extremely high density of squirrels in Vermont likely increased the opportunities for cache pilferage in that system. Finally red squirrels are known to vary in their food caching behaviour throughout their range. Larder-hoarding is the most commonly reported caching tactic in western Canada (Smith 1981, Smith 1968, Rusch and Reeder 1978, Gurnell 1984, Smith and Reichman 1984) and Kluane red squirrels are highly dependent on that larder cache for overwinter survival. However several studies have documented a high degree of scatter-hoarding in eastern Canada (Hurly and Robertson 1990, Dempsey and Keppie 1993). Gerhardt (2005) also suggested that squirrels in his study area may have scatter-hoarded a large proportion of their cones, suggesting less dependence on a single central cache for overwinter survival. A shift in caching strategy from larder-hording to scatter-hoarding, would also shift the focus of territorial defence from a single central midden to a larger more dispersed area of cache sites, and may also increase the opportunity for cache pilferage from the central midden site. Thus, the combination of a young population at high density, with squirrels who may be less dependent on a single central cache, may lead to both more individuals pilfering, and greater opportunities for cache pilferage in Vermont compared to red squirrels in Kluane.

To my knowledge this is the first study to document substantial differences in intraspecific pilfering rates. I have suggested here that age structure and food availability may be important drivers of pilfering rates in a population of food hoarding mammals, and higher pilferage rates could be expected as a decreasing function of territorial defence. Theories on the evolution of hoarding generally support this assumption (Andersson and Krebs 1978); individuals who are better able to defend their cache are expected to be more territorial and larder-hoard, while individuals who are unable to defend their cache from intruders tend to scatter-hoard and do not defend a central place (Andersson and Krebs 1978, Vander Wall 1990, Vander Wall and Jenkins 2003, Dally et al. 2006,). Future studies could quantify the relationship between the energetic investment in the food cache, territorial defence and pilfering rates within a species.

This study has demonstrated that squirrels in Kluane are capable of cache pilfering behaviour when the midden owner is experimentally removed, but this behaviour occurs rarely under natural conditions. Age and food limitation both influence the propensity of an individual to pilfer. The difference in pilfering behaviour in the absence of the territorial owner compared with the low rates of natural pilfering I observed, suggests experiments using artificial food caches should be interpreted with caution for territorial species. Territorial defence, and therefore the opportunity for cache pilferage, likely plays a large role in rates of cache pilferage in food caching animals.

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Table 2-1 Mean index of cones cached ± SE between individuals on the control study grid compared to individuals on the food-addition study grid, for new cones in fall 2008, total cones in fall 2008, and total cones in spring 2009. Independent t-tests assuming unequal variances were used when assumptions of homogeneity of variances were not met (Levene's test) and are denoted by (*). Index of cones cached is calculated by taking the average cones cached in all quadrats and multiplying over the area of the midden (assuming an elliptical shape).

	Study Site		**T-test**		
	Control	**Food-Add**	***df***	**T**	***P***
Mean index of new cones cached (Fall)*	4270.8 ± 710.2	658.6 ± 124.5	36.1	5.010	<0.001
Mean index of total cones cached (Fall)	8206.6 ± 1096.5	5593.2 ± 1051.6	66	1.717	0.091
Mean index of cones cached (Spring)*	89.8 ± 24.9	2115.5 ± 416.8	31.2	-4.852	<0.001

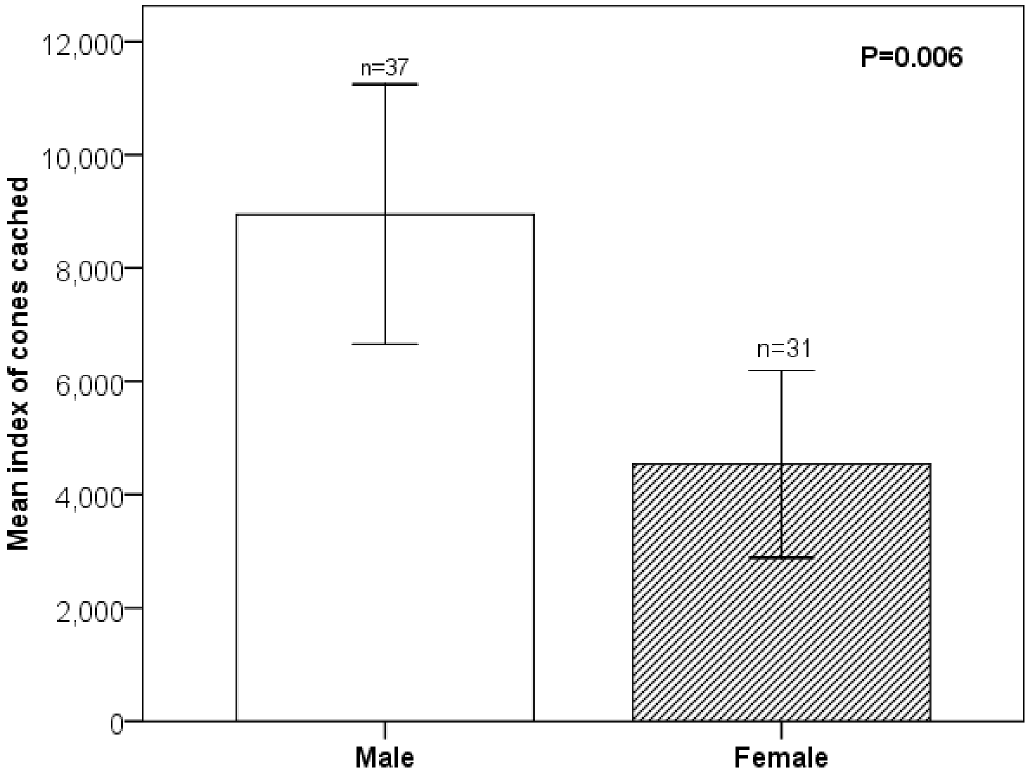

Fig 2-1 Mean index of cones cached ± 2 SE by male and female red squirrels in fall of 2008. Index is calculated by taking an average of all quadrats sampled and multiplying it over the area of the midden (assuming an elliptical shape).

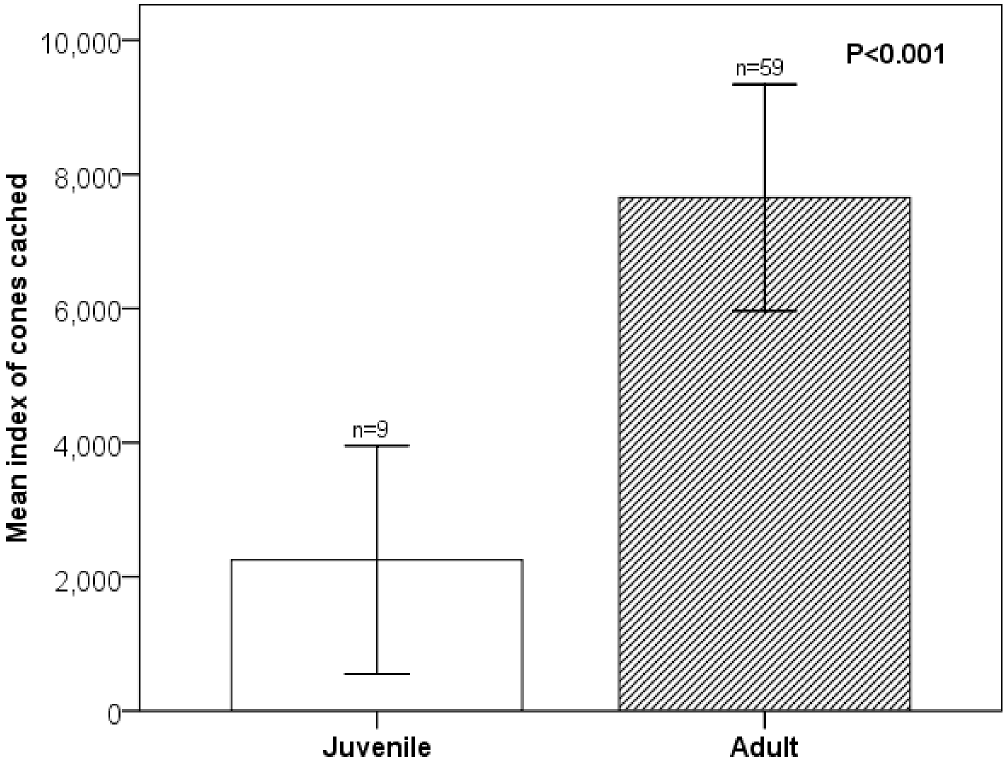

Fig 2-2 Mean index of cones cached ± 2 SE by adult (>1 year) and juvenile (<1) red squirrels. Index is calculated by taking an average of all quadrats sampled and multiplying it over the area of the midden (assuming an elliptical shape).

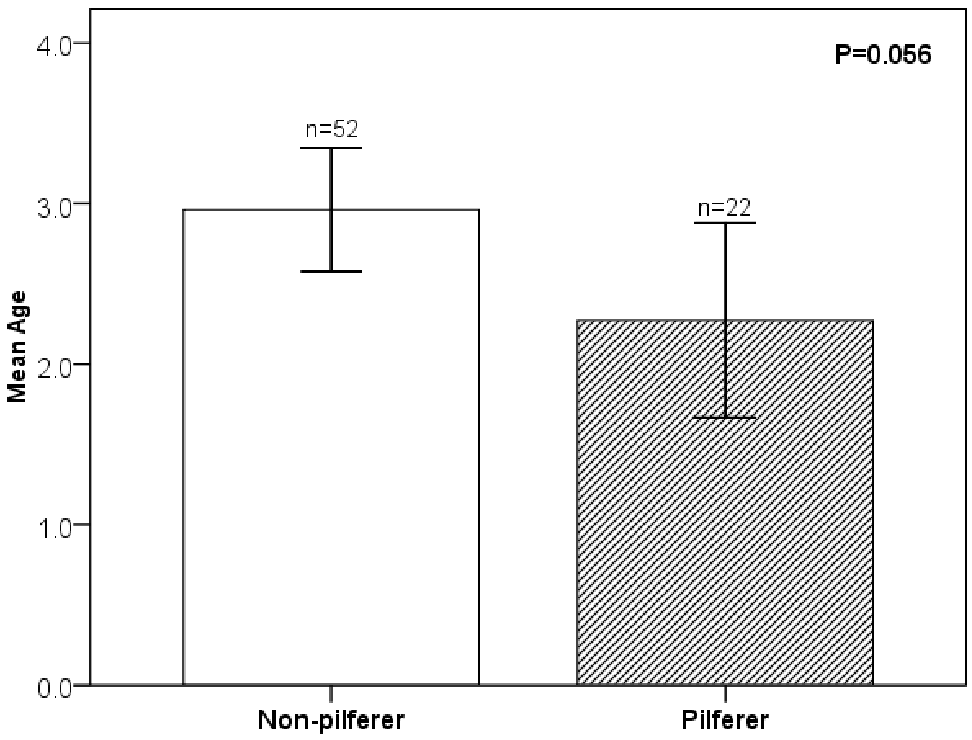

Fig 2-3 Mean age ± 2 SE of squirrels observed pilfering during a removal experiment compared to squirrels that were never observed pilfering.

CHAPTER III

THE INFLUENCE OF FOOD HOARDED ON SURVIVAL IN NORTH AMERICAN RED SQUIRRELS

INTRODUCTION

Food limitation is a common challenge facing animals in temperate environments where food is often seasonally available (Vander Wall 1990). Animals survive food limitation in a variety of ways; they may increase body fat stores, migrate to areas of greater food abundance, enter hibernation or torpor, or they may store food during periods of food abundance for future use during periods of shortage (Vander Wall 1990, Smith and Reichman 1984). Food hoarding is a common strategy that is observed in many mammals; especially rodents (see Vander Wall 1990 for a review). Food hoarding is thought to be a behavioural adaptation to surviving periods of food shortage (Vander Wall 1990, Smith and Reichman 1984, Andersson and Krebs 1978).

Andersson and Krebs (1978) suggest that animals should hoard food when they have a greater probability of recovering that food item than any other individual. The ability to create and recover food caches depends on a variety of ecological, cognitive and physiological mechanisms which influence food caching behaviour (see Vander Wall 1990, Keen-Rhinehart et al. 2010, Smulders et al. 2010). Cache retrieval and cache spacing are the most commonly studied aspects of food hoarding behaviour (Brodin 2010). Fewer studies have focused on quantifying the energetic and survival value of the food cache, and the majority of this research remains theoretical (Pravosudov and Lucas 2001, Hitchcock and Houston 1994). The purpose of this study was to empirically investigate the importance of the food cache to the over-winter survival of red squirrels.

Red squirrels are small food-hoarding mammals that extend throughout the temperate forests of North America (Steele 1998). Red squirrels in western North America are predominantly larder-hoarders, storing most of their food in a large central cache called a midden (Smith 1968a, Gurnell 1984). They are highly territorial, and aggressively defend their middens year-round (Smith 1968a, Gurnell 1984). In the winter months, red squirrels feed primarily on coniferous cones which they have cached in their middens the previous fall. White spruce is a masting conifer species which produces a variable amount of cones each year; ranging from a few cones produced per tree, to all trees synchronously producing hundreds of cones (Dale et al. 2001, LaMontagne and Boutin 2007). For red squirrels in Kluane, YT white spruce is the only coniferous food source available (Dale et al. 2001), and it is estimated to comprise the largest proportion of the red squirrels' diet in this region (Smith 1968b, LaMontagne 2007). Mature spruce cones are only available to be cached for a few weeks in the fall; un-cached cones quickly dry, open, and disperse their seed, making it unavailable to the squirrels. Thus quantifying the number of cones cached in fall provides a good estimate of the amount of food available to the squirrel throughout the winter months.

The primary objective of this study was to quantify the relationship between fall cache size and over-winter survival in red squirrels in Kluane. I counted the number of cones in the middens of known individuals at 2 study sites in fall 2008. Because it has been previously suggested that red squirrels require a cone cache for over-winter survival (LaMontagne 2007, Smith 1968b), I predicted the number of cones cached would be a significant predictor of over-winter survival under natural food conditions. I also considered age, sex, and mass differences in survival. One of these sites is part of an ongoing food supplementation experiment (started in 2004) where most individuals receive 1kg of peanut butter approximately every 6 weeks from October until May. The energy in the supplemented peanut butter provides 3 times the resting metabolic rate of red squirrels (Humphries and Boutin, unpublished data) and should provide squirrels with a surplus of food resources over-winter. Therefore I also investigated if the relationship between cones cached and survival differed at this food supplemented site.

Counting cones in the midden must be done following the fall caching season, requires substantial effort, and is often hampered by early snowfalls. The second objective of this study was to investigate potential surrogate measures of individual food cache size, when time and weather constraints limit the ability to count cones in the midden. Previously, territory size in red squirrels has been correlated with survival (Steury and Murray 2003, LaMontagne 2007). In animals that exhibit food-based territoriality, larger territories are thought to correspond to a greater overall abundance of food (Steury and Murray 2003, LaMontagne 2007, but see Maher and Lott 2000, Adams 2001). Therefore I also investigated the potential for territory size and the number of cones available in trees (territory cone abundance) to be used as a surrogate measures for the amount of food cached in the midden, and examined their ability to predict individual over-winter survival. I predicted that both of these variables would be positively correlated with fall cache size.

METHODS

STUDY SITES

I measured over-winter survival of red squirrels in Kluane, Yukon (61°N, 138°W) between summer 2008 and spring 2009. These populations have been monitored extensively since 1987. A detailed description of the study site and project protocols can be found elsewhere (Berteaux and Boutin 2000, Humphries and Boutin 2000). This study took place on a subset of two research grids, which are staked at 30m intervals and marked with flagging tape. The habitat is open boreal forest dominated by white spruce (Berteaux and Boutin 2000, Humphries and Boutin 2000). In fall 2008 resource conditions in the area were low; trees produced an average of only 2.2 cones and it had been 3 years since a mast cone crop (Boutin and McAdam, unpublished data).

The main study site (control) was an un-manipulated site which experiences natural annual fluctuations in cone availability. Squirrels at the second site (food manipulation) also experience natural annual fluctuations cone availability; however they are also supplemented with peanut butter throughout the winter months. Food supplementation begins in October after fall cone caching is completed. At food supplemented middens a 1 kg yogurt container of peanut butter is suspended in the trees in a large bucket several meters above the primary midden site. Additional containers of peanut butter are added approximately every 6 weeks until May, at which time any remaining peanut butter is removed.

DEMOGRAPHIC VARIABLES

All individuals in the study areas were individually marked at birth, and given uniquely numbered ear tags with coloured markings for visual identification, allowing for complete enumeration of the population. Thus, exact ages of the majority of squirrels in the study areas were known. Newly captured adults were considered to be 1 year old in the year of capture. I obtained weights of all individuals by live-tapping squirrels (using Tomahawk traps baited with peanut butter) in September of 2008, using a Pesola® and handling bag to measure weight (g).

TERRITORY MAPPING

The midden locations of all individuals in the study areas were determined through a bi-annual population census of midden occupancy, as well as periodic live trapping. Territories were mapped by obtaining behavioural observations of the focal squirrel. The location of all territorial behaviours (eating, vocalizing, caching) was recorded by an observer. I obtained an average of 26 observations per squirrel between June and September 2008 for 71 individuals. I generated territory estimates using 95% minimum convex polygons using Home Range Tools for ArcGIS (Ontario Ministry of Natural Resources, Thunder Bay, Canada, 2002). In September 2008 there were 17 males, 13 adult females, and 5 juvenile females on the un-manipulated study site (n=35). On the food supplemented site there were 4 male and 3 female juveniles, 14 adult males and 12 adult females (n=33).

OVER-WINTER SURVIVAL

To determine over-winter survival, I used data from spring 2009 trapping records and the spring midden census of the Kluane Red Squirrel Project. During this census all known middens are trapped and monitored for red squirrel activity, and individual owners are identified using behavioural cues such as rattle calls, barking, and frequent trapping at the site. Squirrels no longer present in the population after May 1st 2009 were considered deceased.

TERRITORY CONE AVAILABILITY

In August 2008 I counted cones on 4116 trees within the study areas; 2562 in the control study area and 1554. Cones were counted on the three trees closest to pre-existing grid markers which are at 30 X 30 m spacing across the grid. For a more fine-scale estimate of cone production in squirrel territories I counted cones using transect sampling. A 15 m transect, which originated at the midden centre, was placed in each of the cardinal directions. The 2 closest trees to the transect line were counted every 5 m extending out from the midden. To ensure no tree was counted twice, I marked all counted trees with flagging tape.

Cones were counted on trees which were greater than 5 cm DBH and were in good health (no spruce beetle attack). To count cones an observer stood 15-20 m from the base of the tree and counted all visible cones within 3 metres of the top of the tree using binoculars (LaMontagne 2007, LaMontagne et al. 2005). The number of visible cones was converted to total cones using the equation total cones= 10^ (0.073 + 1.189 • log (visible cones)) (LaMontagne et al. 2005).

I used Inverse Distance Weighting (power=1, maximum distance=90m) in ArcGis 9 (Environmental Systems Research Institute Inc., Redlands, California, 2008) to interpolate cone production in the study area in 2008. I then used the Zonal Statistics Tool (Environmental Systems Research Institute Inc., Redlands, California, 2008), to extract an estimate of total cones available to each squirrel based on the 95% minimum convex polygons of each territory in the study area.

MIDDEN CACHE SIZE

I estimated the number of spruce cones hoarded by red squirrels following the caching season in fall 2008. The cache size in the primary midden of each individual in the study areas was estimated using quadrat sampling. The midden was separated into 4 quadrants by marking an X through the centre of the midden. Four 0.6 X 0.6 m quadrats were placed within each quadrant at equal spacing. All closed spruce cones inside the quadrat, to a maximum depth of 20 cm, were counted. Cones of the year (new) were distinguished from cones from previous years (old) based on colouration; new cones were purple-green while old cones were brown. The length and width of the midden were measured and used to estimate the area of the midden (assuming an elliptical midden shape). The number of cones found in each quadrat was averaged and multiplied by the estimated area of the midden to estimate total cache size.

STATISTICAL ANALYSIS

All analyses were carried out using SPSS 16.0 (SPSS Inc. Chicago, IL USA). I used an information-theoretic approach to model selection (Burnham and Anderson 2002) to identify variables important to the over-winter survival of red squirrels in this region. Models included variations of the following parameters: sex, age, mass, territory size, cones available (by territory), and old cones cached, new cones cached, or total cones cached. Tolerance and variance inflation factor analyses indicated there was low collinearity between predictor variables (for all parameters tolerance>0.1, VIF<2). Preliminary analysis using Binary Logistic

Regression in SPSS to test for statistically significant interactions revealed no significant interaction terms; therefore no interactions were included in the models. Twenty-seven potential models, based on a priori predictions, and a null model were evaluated using Generalized Linear Modeling with a binary logistic logit link. I used Akaike's Information Criterion for small sample size (AICc) to rank my models' ability to predict over-winter survival. Data on cones cached, territory cones, and territory size were natural log transformed to meet with the assumptions of normality. For the unmanipulated site, squirrels that were age 4, 5 and 6 were collapsed into a single age category (>3), because of limitations of sample size at ages 5 and 6. For the food-manipulated site, squirrels that were age 5 to 7 were similarly collapsed into a single category (>4) because of limitations in sample size. I excluded 5 individuals from the modeling exercise for the food manipulation site, because the middens they were defending in fall 2008 did not have peanut butter feeders.

General Linear Univariate models with Tukey's post hoc tests were used to analyze differences in food cache size between males and females, and across age classes at the two sites. I used regression to determine if territory size and the number of cones available in 2008 were significantly related to the number of cones red squirrels had cached in their middens.

RESULTS

Control Site:

Density of squirrels at the control site in fall 2008 was 1.9 squirrels per hectare. There was no significant difference in the number of cones cached between males and females ($F_{1, 28}$=2.389, p=0.133; Figure 3-1). Age had a significant effect on the number of cones cached ($F_{3, 28}$=6.436, p=0.002); with older squirrels tending to have more cones cached than juvenile squirrels (Figure 3-1). On average the new cones cached by red squirrels comprised 57.0 ± 33.6% (SD) of the total cones in the midden. Mean ± SE cache size of squirrels that survived winter was 8361.6 ± 1169.0. Squirrels who did not survive over-winter had an average of 6559.4 ± 2660.0 cones cached in their middens.

Over-winter mortality of squirrels who held a territory in fall 2008 was 32.4% (11/34); 4 adult males, 5 adult females, and 2 female juveniles did not survive over-winter. Neither of the deceased juveniles had any cones cached in their middens in fall 2008. Five adult squirrels (4 females and 1 male) had less than 3000 cones cached; all of these squirrels were 3 or 4 years of age. The remaining deceased squirrels (1 female, 3 males) had more than 10000 cones cached; these squirrels were 4 to 6 years of age.

Table 3-1 summarizes the AICc rankings of the 27 a priori models predicting over-winter survival in red squirrels. The model with the most support included age and midden cache size (Table 3-1). Parameter estimates for covariates of over-winter survival, odds ratios, and confidence intervals of the top model are presented in Table 3-2. The amount of cones cached in the midden had an odds ratio and 95% confidence interval of less than one (Table 3-2), indicating the number of cones cached had a negative influence on squirrel mortality, or for each one unit decrease in cones cached (on a natural log scale) squirrels were 22.5% less likely to survive the winter (Figure 3-2). The odds ratio and confidence intervals for age were greater than one (Table 3-2), indicating a one year increase in age resulted in a 91.0% increased probability of mortality over-winter (Figure 3-3).

There was no relationship between the territory size and the number of new cones cached ($F_{1, 33}$=1.743, R^2=0.050, p=0.196). There was a weak positive relationship between territory size and the number of old cones cached ($F_{1, 33}$=3.110, R^2=0.086, p=0.087), and the total (new and old) number of cones cached in the midden ($F_{1, 33}$=3.113, R^2=0.086, p=0.087). There was no relationship between the number of new cones cached and the estimated cone abundance on the territory ($F_{1, 32}$=3.118, R^2=0.086, p=0.086).

Food Manipulation Site:

In fall 2008 density on the food manipulated site was 4.4 squirrels per hectare. There was no significant difference in the number of cones cached between males and females ($F_{1, 24}$=0.072, p=0.791; Figure 3-4). Age had a significant effect on the number of cones cached ($F_{4, 24}$=3.654, p=0.018); juveniles had fewer cones than adults (Figure 3-4). On average, old cones represented 79.8 ± 24.3% (SD) of the total cones cached on the midden. Squirrels who survived over-winter had an average of 6440.0 ± 1258.4 (SE) cones cached in their middens. All but one of these squirrels was food supplemented and received peanut butter throughout the winter months. Squirrels who did not survive over winter had 2223.9 ± 1146.9 (SE) cones cached.

Over-winter mortality of squirrels who held a territory in fall 2008 was 21.2% (7/33) on this site; 2 male juveniles, 4 yearlings (1 male and 3 females), and one 4 year-old female. All but one of these squirrels had less than 3000 cones cached in their middens. Three of the 7 squirrels were not food supplemented, as they did not have bucket feeders on their middens. A Pearson Chi-square test suggests that squirrels who had a bucket feeder were much more likely to survive the winter than squirrels who did not have a bucket feeder (X^2_{32}=7.549, p=0.006). Only one individual who did not have a bucket feeder survived the winter.

Table 3-3 summarizes the AICc rankings of the 27 a priori models predicting over-winter survival in red squirrels who received supplemental food. No single model of over-winter survival of food-supplemented squirrels had sufficient support; Akaike weights were all less than 0.2 and the $\Delta AICc$ differed by less than 2 between the top models. Therefore I used model averaging to estimate the importance of the parameters to the over-winter survival of red squirrels that were food supplemented. Model averaged parameter estimates for covariates of over-winter survival, odds ratios, and confidence intervals are presented in Table 3-4. There was little support for any of the parameters I tested; all confidence intervals of the odds ratios bound 0, and therefore have no detectable influence on mortality of food supplemented squirrels.

There was no relationship between the territory size and the number of new cones cached ($F_{1, 30}$=0.014, R^2=0.000, p=0.908). Unlike on the control grid, there was also no relationship between territory size and the number of old cones cached ($F_{1, 30}$=0.269, R^2=0.009, p=0.608), or the total (new and old) number of cones cached in the midden ($F_{1, 30}$=0.127, R^2=0.004, p=0.724). There was no relationship between the number of new cones cached and the estimated cone abundance on the territory ($F_{1, 30}$=0.013, R^2=0.000, p=0.910).

DISCUSSION

My results suggest that food and age were the most important factors influencing over-winter survival of red squirrels between fall 2008 and spring 2009 under natural food conditions. Squirrels that had smaller food caches were less likely to survive the winter than squirrels with larger food caches. Older squirrels were also less likely to survive winter then younger squirrels. Mass, sex, territory size and the number of cones available on a territory were poor predictors of over-winter survival during this study. Parameters which were important to survival under natural conditions were not found to be important under food-manipulated conditions. On the experimental grid, the best predictor of over-winter survival was if a squirrel owned a midden with a peanut butter feeder, suggesting that food addition changes the relationship between food hoarded and over-winter survival in red squirrels.

Results from the study of squirrels under natural food conditions support my hypothesis that the midden food cache is important for the over-winter survival of red squirrels. During this study individuals who had no cones cached in September 2008, did not survive over-winter. The survival model estimated squirrels with no cones cached (non-hoarders) had a 100% probability of death over-winter, while squirrels with an average-size cone cache (7795 cones) had only a 8.1% probability of not surviving the winter (holding age constant). I have empirically demonstrated that the food cache is important for over-winter survival for larder-hoarding red squirrels in Kluane. Previous work in this system has linked fall cone abundance (in the entire study area) with reproductive success (Humphries and Boutin 2000, McAdam and Boutin 2003a, McAdam et al. 2007). For red squirrels in this system, food hoarding is an important strategy to survive winters of food shortage, and provides resources to allocate to reproduction in the spring. Thus quantifying differences in individual variation in food cache size may also explain some individual variation in reproductive success. I have demonstrated that the amount of cones cached increases the probability of over-winter survival in red squirrels; however more research is needed to understand the importance of individual cache size in other aspects of life-history such as reproduction.

Age was also a strong predictor of over-winter survival. On the control site the average lifespan of a female red squirrel who has survived past her first year was 3.5 years, with a maximum recorded life span of 8 years (McAdam et al. 2007). In the year of this study, 2 year-old red squirrels had 85.8% probability of survival; however, the probability of survival after 3 and 4 years was only 37.6% and 42.2% respectively. These results are consistent with McAdam et al. (2007), who found survival of 772 females born between 1987 and 1997 was highest in 2 year olds and declined thereafter. Descamps et al. (2008) also found survival models had the highest statistical support when they included age. However, predictions of juvenile survival from my model do not agree with previous studies (McAdam et al. 2007, McAdam and Boutin 2003b, Larivee et al. 2010), which have consistently found high juvenile mortality. Juvenile survival in this system is generally low; from 1989 to 2001 the average probability of survival to 1 year was only 0.25 (McAdam and Boutin 2003b), and McAdam et al. (2007) found only 26% of offspring produced survived to 1 year of age. This is largely because juveniles must have a midden to survive the winter (Smith 1968a, Larsen and Boutin 1994). My model underestimates juvenile mortality because only juveniles who survived the summer, and were defending a territory in fall 2008, were included in the model. The model is further limited by low sample size of juvenile squirrels. Also, McAdam and Boutin (2003b), McAdam et al. (2007), and Descamps et al. (2008) estimated probability of survival over many years (20, 18 and 14), encompassing a wide range of population densities and resource levels. My model only estimates survival over a single winter, and therefore the results are constrained within the resource and density conditions of that year and may not be representative of the population over multiple years. Overall, the results from this study strongly support an increase in mortality risk after age 2 that is consistent with previous findings, but predictions for juvenile mortality should be interpreted with caution because of the limitations of the study design.

On the control site all juveniles who held a territory with cones (n=3) survived the winter, while those who did not have any cones died (n=2). Older squirrels (>3 years) who died (n=7) did not seem to be limited by food; all but 2 had more than the predicted 7300 cones needed to survive over-winter (LaMontagne 2007). This suggests that while survival for all squirrels is dependent on defending a territory with an adequate food hoard, mortality in older squirrels, which have maintained and defended a midden for multiple years, may be more strongly driven by other factors. Previous studies in this system have demonstrated both higher costs of reproduction for older squirrels (Descamps et al. 2009) and senescence (Descamps et al. 2008), and these factors likely account for the increased mortality of older squirrels observed here.

Sex and mass were not significant predictors of over-winter survival during this study. Descamps et al. (2008) found that body-mass increases in red squirrels until age 4, then remains constant. Thus mass should be a poor predictor of mortality in squirrels over 4 years. Mass is known to affect juvenile survival (Larivee et al. 2010); however the number of juveniles included in this study limits my ability to detect a mass effect on survival of young squirrels. During this study similar numbers of males and females did not survive over-winter; therefore I detected no sex differences in mortality. Descamps et al. (2008) found males and females showed different patterns of survival; females showed age-variation in survival after 3 years, while males did not show age-variation except in males >7 years. The sample size in this study limits my ability to test interactions between age and sex, and therefore to detect survival differences between the sexes if they exist. In general a higher sample size of both juveniles and old squirrels (>3) would allow stronger conclusions about the influence of sex and mass on over-winter survival under natural food conditions.

Under food manipulated conditions, I found no support for any of the models used to predict over-winter survival under natural conditions. The only predictor of over-winter survival on the manipulated site was whether or not a squirrel owned a peanut butter feeder. The food addition experiment currently underway (since 2004) seems to be effectively manipulating the resource conditions available to squirrels in the study area; unlike in the control study area, the number of cones hoarded by squirrels on the experimental site does not influence their survival outcome. The food supplementation also seems to be influencing age structure of the population; there was a single death among individuals older than 2 years during the study period, compared to the control study area where squirrels older than 2 comprised 81.8% of the mortalities. From this preliminary analysis, it appears food supplementation is altering the relationship between the amount of food hoarded and over-winter survival in red squirrels.

During this study I also examined the potential to use surrogate measurements for the amount of cones hoarded by red squirrels. I found territory food abundance was a poor predictor of both survival and the number of cones cached. This measure does not account for cones cached in previous years and is therefore not a meaningful representation of resources available in the midden. Although territory size was also not a good predictor of survival, it was weakly correlated with the total amount of cones squirrels cached (under natural conditions). Previous studies have found a significant relationship between survival and territory size in red squirrels (LaMontagne 2007, Steury and Murray 2003). Data from this study suggest that territory size did not reflect current resource conditions in fall 2008 (measured by new cones cached), and explained only 8.6% of the variation in total number of cones cached on the control site. Territory size is only a weak predictor of food hoarded for a variety of reasons: (1)

cone production within a given size of territory can be highly heterogeneous, especially in areas that have been affected by spruce beetle attack (personal observation), and cone production within a territory can vary considerably from year to year (LaMontagne 2007), (2) data from this study suggest 43.0% cones in midden are from previous years (control site), (3) territory size in red squirrels fluctuates with density and territories tend to be larger at low density after accounting for food availability (LaMontagne 2007, Steury and Murray 2003), and (4) the cone harvesting effort by red squirrels may vary between individuals. These factors confound the relationship between the size of an individual's territory and the amount of food they have cached in a given year, therefore I caution the use of individual territory size as a surrogate measure of individual food resources in these hoarding animals.

The purpose of this study was to examine the relationship between the amount of food hoarded and survival in 2 populations of red squirrels. Under natural conditions, age and the amount of food stored significantly influenced the probability of survival in red squirrels. This model was limited by both sample size and study-period, and would be improved by collecting data over multiple years. The results of this study also suggest that food supplementation alters the relationship between midden cache size and over-winter survival, and may allow individuals to survive who normally would not under natural conditions. In addition to the predictions of the models, I have suggested that territory size alone may be a poor surrogate measure of individual food resources because it does not account for many of the factors that influence fall cache size. This study has empirically demonstrated that the larder-cache of hoarded spruce cones is necessary for over-winter survival in red squirrels under natural conditions, and has highlighted the need for further empirical research into understanding the evolution of food-caching to survive periods of food shortage in other animals.

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Table 3-1 AICc ranking of models of over-winter survival (2008-2009) in red squirrels under natural food conditions. Models are derived from a generalized linear logistic regression model.

Models	**K**	**AIC**	**AICc**	Δ_i	**w**$_i$
Age + ln(Midden Cones)	3	30.24	31.16	0.00	0.48
Mass + Age+ ln(Midden Cones)	4	31.79	33.39	2.23	0.16
Sex + Age + ln(Midden Cones)	4	32.35	33.68	2.52	0.14
Mass + Age+ ln(Midden Cones) + ln(Territory)	5	33.77	35.84	4.68	0.05
Mass + Age + Sex + ln(Midden Cones)	5	33.76	35.99	4.83	0.04
Age + ln(Old Cones) + ln(New Cones)	4	34.82	36.15	4.99	0.04
Mass + Age	3	36.23	37.15	6.00	0.02
ln(Midden Cones)	2	37.06	37.50	6.34	0.02
Mass + Age+ ln(Midden Cones) + ln(Territory Cones) + ln(Territory)	6	35.75	38.75	7.59	0.01
ln(Midden Cones) + ln(Territory Cones)	3	38.98	39.90	8.74	0.01
Sex + ln(Midden Cones)	3	39.06	39.98	8.82	0.01
Mass + ln(Midden Cones)	3	39.06	39.98	8.82	0.01
Age + ln(Old Cones)	3	39.84	40.62	9.46	0.00
ln(Territory Cones)	2	40.65	41.10	9.94	0.00
Age + ln(New Cones)	3	40.45	41.22	10.06	0.00
Mass + Age + ln(Old Cones)	4	40.14	41.47	10.31	0.00
Mass + Age + ln(New Cones)	4	41.22	42.55	11.40	0.00
ln(Midden Cones) + ln(Territory)	3	43.11	43.89	12.73	0.00
ln(Old Cones)	2	45.18	45.55	14.39	0.00
ln(New Cones)	2	45.86	46.06	14.90	0.00
Age	2	46.12	46.50	15.34	0.00
Null model	1	45.57	47.13	15.97	0.00
ln(Old Cones) + ln(New Cones)	3	46.46	47.23	16.07	0.00
Mass + Age + ln(Territory)	4	46.29	47.63	16.47	0.00
Age + Mass + Sex	4	46.74	48.08	16.92	0.00
Mass + Age+ SEX + ln(Midden Cones) + ln(Territory Cones) + ln(Territory)	7	41.83	48.57	17.41	0.00
Mass + Age + ln(Territory) + ln(Territory Cones)	5	48.15	50.22	19.06	0.00
ln(Old Cones) +Sex	3	47.17	47.94	16.78	0.00

Table 3-2 Summary of best AICc model from generalized linear model logistic regression predicting over-winter survival in red squirrels experiencing natural food conditions from 2008 to 2009. Death is modeled as the response variable. All odds ratios are significantly different from one based on 95% confidence intervals.

Covariate	Coefficient	Confidence interval		Odds Ratio	95% CI Odds Ratio	
ln(Midden Cones)	-1.24	-2.38	-0.101	0.29	0.09	0.90
Age	2.31	0.04	4.5851	10.11	1.04	98.01

Table 3-3 AICc ranking of models of over-winter survival (2008-2009) in red squirrels under manipulated food conditions. Models are derived from a generalized linear logistic regression model.

Models	**K**	**AIC**	**AICc**	Δ_i	w_i
ln(Old Cones)	2	21.49	21.97	0	0.15
ln(Midden Cones) + Sex	3	21.21	22.21	0.24	0.14
ln(Old Cones) + Sex	3	21.27	22.27	0.31	0.13
ln(Midden Cones)	2	21.99	22.55	0.58	0.12
ln(Old Cones) + ln(New Cones)	3	22.81	23.81	1.84	0.06
ln(Old Cones) + Age	3	22.99	23.99	2.02	0.06
ln(Midden Cones) + ln(Territory)	3	23.09	24.09	2.12	0.05
Age + ln(Midden Cones)	3	23.50	24.50	2.53	0.04
Age	2	24.24	24.72	2.75	0.04
ln(Midden Cones) + ln(Territory Cones)	3	23.84	24.84	2.87	0.04
Mass + ln(Midden Cones)	3	23.99	24.99	3.02	0.03
Age + ln(Old Cones) + ln(New Cones)	4	23.78	25.52	3.55	0.03
Mass + Age + ln(Old Cones)	4	24.99	26.73	4.76	0.01
Mass + Age + Sex + ln(Midden Cones)	5	24.42	27.15	5.18	0.01
Age + ln(New Cones)	3	26.17	27.17	5.2	0.01
Mass + Age+ ln(Midden Cones)	4	25.48	27.22	5.25	0.01
Mass + Age	3	26.23	27.23	5.27	0.01
ln(New Cones)	2	26.24	27.24	5.28	0.01
ln(Territory Cones)	2	26.81	27.29	5.33	0.01
Null model	1	25.12	27.30	5.33	0.01
Age + Mass + Sex	4	26.27	28.01	6.04	0.01
Sex + Age + ln(New Cones)	4	26.30	28.04	6.07	0.01
Mass + Age + ln(Territory)	4	26.95	28.69	6.72	0.01
Mass + Age+ ln(Midden Cones)+ ln(Territory)	5	26.34	29.07	7.1	0.00
Mass + Age + ln(New Cones)	4	28.17	29.90	7.94	0.00
Mass + Age+ Sex + ln(Midden Cones) + ln(Territory Cones) + ln(Territory)	7	25.46	31.06	9.09	0.00
Mass + Age + ln(Territory) + ln(Territory Cones)	5	28.75	31.47	9.5	0.00
Mass + Age+ ln(Midden Cone) + ln(Territory Cones) + ln(Territory)	6	28.24	32.24	10.3	0.00

Table 3-4 Summary of model-averaged AICc model from generalized linear logistic regression predicting over-winter survival in red squirrels that have been supplemented with food. Death is modeled as the response variable. All odds ratios are not different from one.

Covariate	**Coefficient**	**Confidence Interval**		**Odds Ratio**	**95% CI Odds Ratio**	
Age	-0.66	-2.14	0.83	0.52	0.12	2.29
ln(Midden Cones)	-0.98	-2.14	0.18	0.37	0.12	1.19
ln(New Cones)	0.24	-0.55	1.03	1.27	0.58	2.80
ln(Old Cones)	-0.92	-1.87	0.02	0.40	0.16	1.02
ln(Territory Cones)	-0.22	-1.62	1.19	0.81	0.20	3.28
ln(Territory)	-0.75	-2.29	0.80	0.47	0.10	2.21
Mass	0.01	-0.06	0.07	1.01	0.94	1.07
Sex	2.37	-1.25	6.00	10.73	0.29	401.87

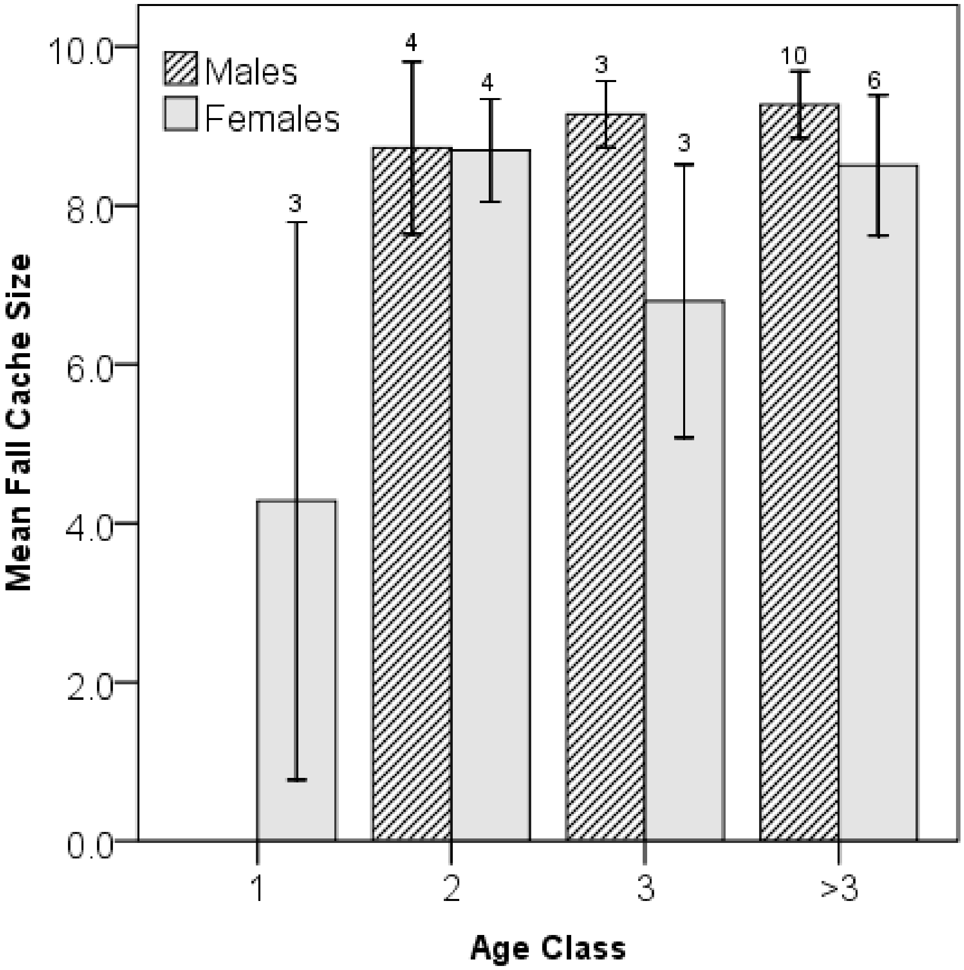

Figure 3-1 Natural log of the mean number of cones cached by red squirrels in fall 2008 ± 2 SE by age and sex under natural food conditions. The category >3 includes squirrels who are 4, 5 & 6 years of age. Numbers above error bars indicate sample size.

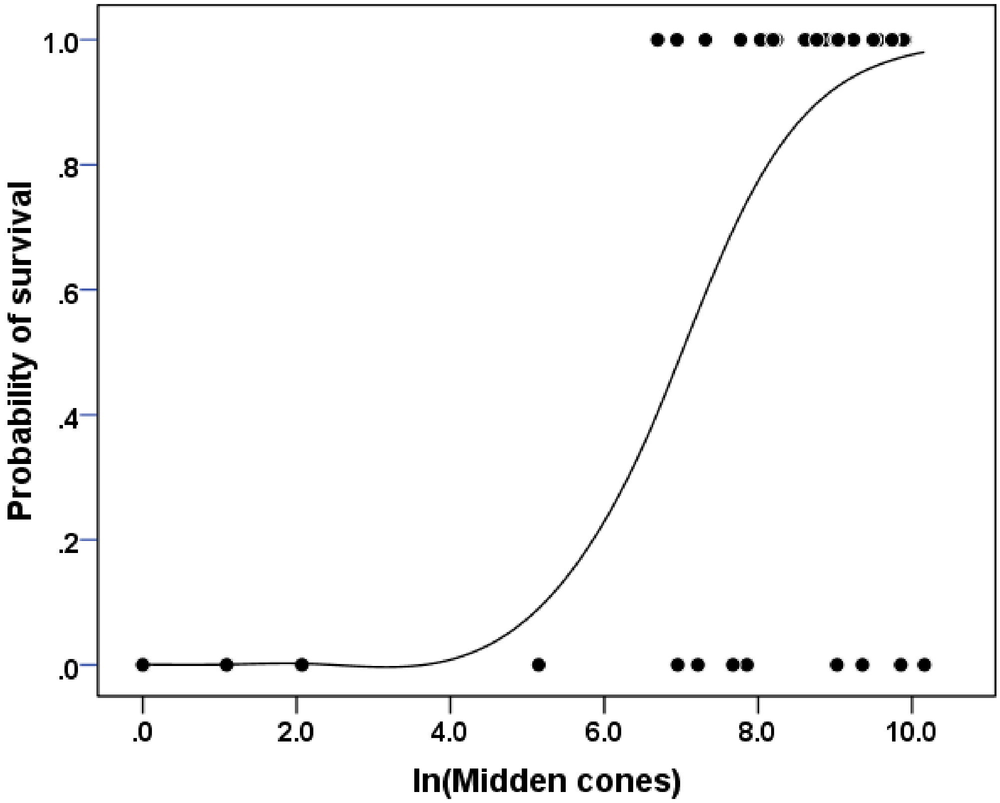

Figure 3-2 Probability of survival for red squirrels under natural food conditions between fall 2008 and spring 2009 based on the natural log of the number of cones hoarded in fall 2008. Cache size parameters are calculated from the top AICc model (survival= age and ln(midden cache size)), while holding age constant. Black dots indicate individual survival outcomes (n=34).

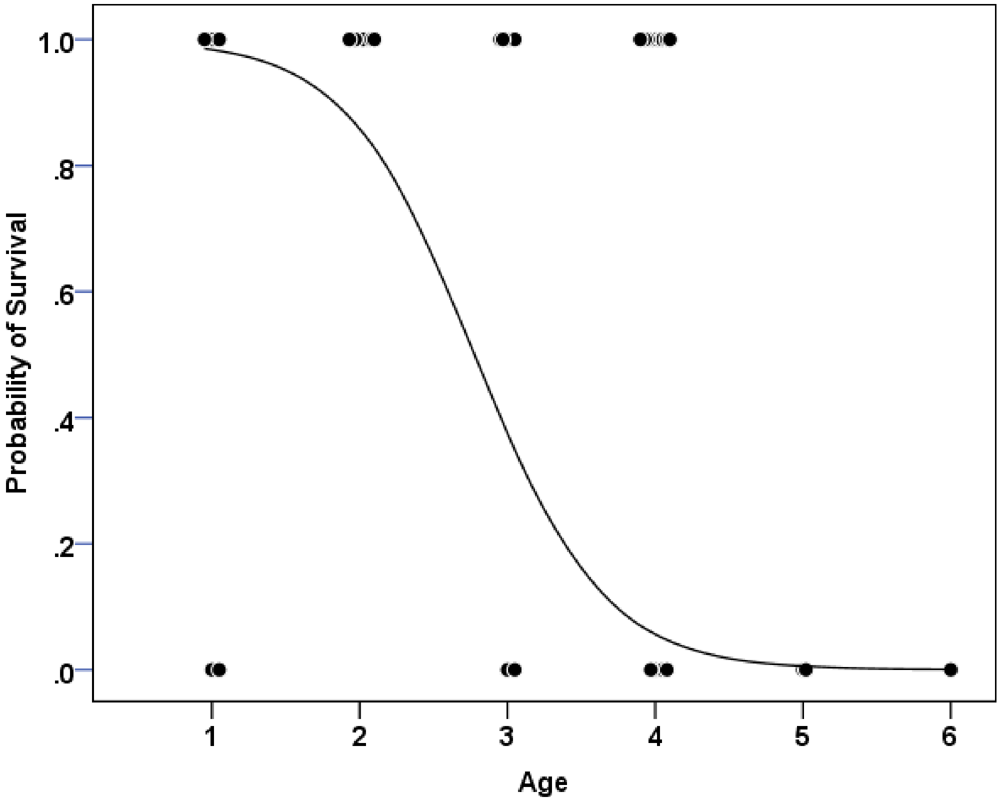

Figure 3-3 Probability of survival by age for red squirrels under natural food conditions from fall 2008 to spring 2009. Probabilities are calculated from the top AICc model (survival= age and ln(midden cache size)), while holding ln(midden cones) constant. Black dots indicate individual survival outcomes (n=34).

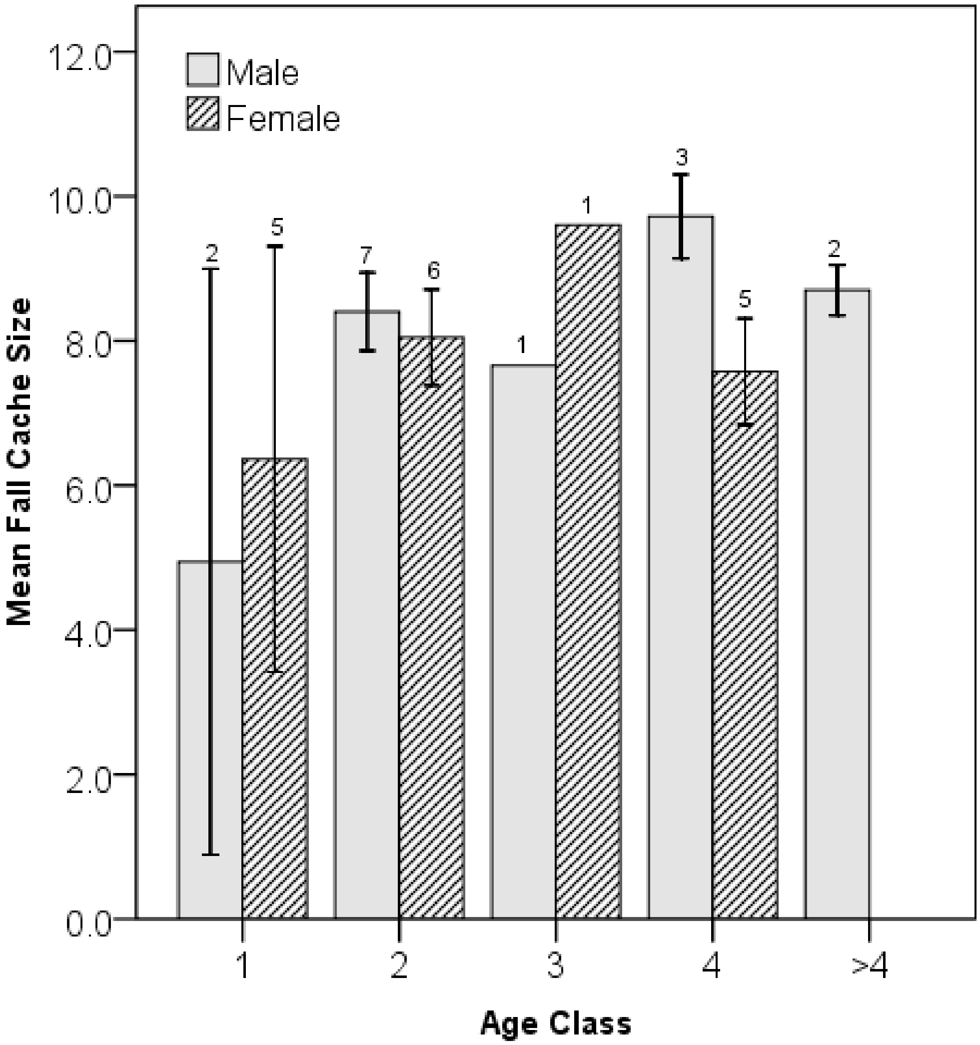

Figure 3-4. Natural log of the mean number of cones cached by red squirrels in fall 2008 ± S.E. by age and sex under manipulated food conditions. Number above error bars indicate sample size.No error bars are presented for age class 3 because n=1. The category >4 includes squirrels age 5 and 7.

CHAPTER IV

GENERAL DISCUSSION AND CONCLUSIONS

Pilfering is a common behaviour in food hoarding animals (Vander Wall 1990), and is suggested to account for up to 30% of cache losses (Vander Wall and Jenkins 2003). Such large losses of resources can influence both the survival and reproductive success of individuals, and are generally thought to lead to increased spatial dispersion of the food cache (scatter-hoarding). However, these estimates are largely based on studies of artificial food caches, and pilfering is very rarely studied in wild populations. Among food hoarding species that have been studied in the wild (McKechnie et al. 1994, Gerhardt 2005, Edelman et al. 2005), reported rates of cache pilferage vary greatly between study sites. Thus, while there is plenty of evidence that many species have a propensity for cache pilferage, natural rates of cache pilferage and the underlying mechanisms that motivate pilfering behaviour are less clear.

The main objective of this study was to estimate cache pilferage rates in a population of larder-hoarding red squirrels, and to understand how resource abundance and other demographic variables may influence pilfering rates both within and among populations. I accomplished these objectives by estimating pilfering rates using a mark-recapture approach to following pilfered spruce cones, and experimentally manipulating territorial defence to observe the propensity of individual squirrels to pilfer. I also quantified the size of the fall food cache, and examined its importance for over-winter survival to better understand how resources may influence pilfering behaviour. Examining the underlying drivers of pilfering behaviour provides a better understanding of how the defence and competition for resources influences food-caching strategies. Overall this study investigates the variation in rates of cache pilferage between individuals and among populations, and provides insights into the role of age and food resources in the propensity for cache pilferage in red squirrels.

SUMMARY OF RESULTS

Red squirrels in Kluane, Yukon are capable of cache pilferage, but pilfering under natural conditions is rare in this region. In 2008 red squirrels had an average of approximately 7 000 cones, but some squirrels had more than 20 000 cones cached. Middens contained both new cones and cones from previous years. Males had significantly more cones cached than females, and younger squirrels had fewer cones than older squirrels. Only squirrels who were defending a midden in the fall survived the winter, and squirrels with larger cone caches were more likely to survive. Variation in midden cache size was common within populations, and influenced the over-winter survival of red squirrels in this region, suggesting the larder-cache is an important commodity to defend.

During the removal experiment I observed midden intrusions in 70% of trials and squirrels removed food items in 74% of those trials. Male and female red squirrels were equally likely to pilfer. Younger squirrels were more likely to pilfer than older squirrels, and pilfering squirrels had fewer cones cached than squirrels that were not observed pilfering. Squirrels who pilfered during the removal experiment were significantly less likely to survive over-winter, suggesting that pilfering is more common among young and poor quality individuals who have inadequate food caches.

I recovered evidence from 63% of cones marked on middens in 2008. Between October 2008 and April 2009, I detected pilfering by only 14% of squirrels in the study area. These squirrels stole an average of 2.1% of their total food cache; however these stolen cones represented only 0.3% of all the cones cached in middens in the study areas that year. I detected no unique characteristics of pilfering in these squirrels, but this was strongly influenced by low sample size. Many pilfering events were at middens where the owner had died at some point during the winter. Sixteen percent of squirrels lost cones to pilfering, which represented approximately 2.1% of the cones they had cached. The pilfering squirrel was always from a neighbouring midden. Overall, cache pilferage under natural conditions appears to be a very rare behaviour, and the number of cones gained or lost to stealing does not seem to have a large effect on the overall amount of food a squirrel has hoarded.

The rate of cache pilferage in a population depends on both the propensity for cache pilferage and the opportunity for cache pilferage. The results of this study have demonstrated that red squirrels in Kluane, YT are likely to engage in pilfering when given the opportunity, and that pilfering is more common in young squirrels and those who have fewer food resources. However, the very low rates of cache pilferage at the population level suggest that red squirrels in Kluane are very effective at excluding potential intraspecific competitors from their middens and thus limit the opportunity for cache pilferage. This high degree of territorial defence is likely related to the importance of the midden for over-winter survival in this region.

FUTURE DIRECTIONS

Kleptoparasitism is common in many group-living birds and food-hoarding mammals (Brockmann and Barnard 1979, Iyengar 2001, Vander Wall and Jenkins 2003, Dally et al. 2006, Iyengar 2008); however research about the role of kleptoparasites in a population or community remains largely theoretical. Among food-caching mammals, most studies examine pilfering rates from artificial caches, and few estimate natural rates of cache pilferage. The evolution of cache spacing behaviours (larder-hoarding vs. scatter-hoarding) is believed to be related to the ability to defend a cache from pilferage; however these theoretical predictions remain largely untested. To begin to address these questions empirically more studies need to identify natural rates of cache pilferage and the underlying mechanisms that may drive pilfering behaviours.

Larder-hoarding red squirrels in Kluane are a good study species to address questions about pilfering and caching behaviour, because they are easily monitored and their food resources can be quantified and tracked. This study identified some characteristics of pilfering squirrels and found low rates of cache pilferage. By studying pilfering in this system over multiple years under different resource conditions and squirrel densities, the mechanisms driving the rates of cache pilferage may become clearer. Ideas of areas of further research that have arisen during the course of this work are listed below:

- Are pilfering rates within a population different at other times of year such as spring or summer?
- Is there more pilfering at higher densities?
- Why do squirrels pilfer mushrooms? Are mushrooms a limited resource to squirrels? Do mushrooms provide some limited nutrient or mineral?
- Sample size limited my ability to study if pilfering squirrels have distinctive personalities. Future research could use the growing amount of personality data from the Kluane Red Squirrel Project to examine personality differences in pilfering and non-pilfering squirrels

- Is pilfering an inherited trait? When examining the genetic pedigree of red squirrels in the study site, there is some indication that pilfering individuals have other family members who also pilfer. More data over multiple generations would be required to fully address this question.

- How does territorial defence of the midden limit the opportunity for cache pilferage? Do squirrels know when their neighbours are away? Do squirrels that get stolen from differ in their defence of the midden?

- Is the amount of time spent defending the midden based on the size of the food cache? Are squirrels with larger food caches more likely to defend their middens compared to squirrels with fewer resources?

- How does territorial defence of a midden change in populations of squirrels that tend to scatter-hoard and larder-hoard? Is there greater opportunity for cache pilferage in squirrels that both scatter and larder-hoard?

- Why is there a gradient of scatter-hoarding to larder-hoarding from east to west? Does pilfering play a role in this gradient? Are squirrel in the east more likely to pilfer than squirrels in the west?

- Do pilfering rates differ as a function of the value of the food item? Is there more pilfering in areas with more nutritious cones?

- Are squirrels aware of how many cones they have cached? Why do squirrels manage cached cones (i.e. stack them and orient them all in the same direction)? Do cones effervesce to the surface over time? Do squirrels remember cache locations or do they use their senses to detect them? How many years are cones viable in the midden?

- Why do females have fewer cones cached than males? Do they deplete cone caches more quickly? Do they have lower quality territories?

- How does fall cache size relate to reproductive success in the following spring?

- Despite the clear influence of food supplementation on survival, red squirrels continue to cache cones in the fall and continue to defend sizable larder-caches of spruce cones. The food supplementation experiment currently underway provides an opportunity to further investigate the drivers of caching behaviour, as food shortage is experimentally eliminated.

This study examined the natural rates of cache pilferage in red squirrels and some of the factors that may drive individuals to steal. Although I have demonstrated that both resources and age are important drivers in pilfering behaviour, many questions remain unanswered. Measuring pilfering is difficult and time consuming, but more studies of natural cache pilferage are needed to fully understand how pilfering influences food caching behaviour, and why pilfering rates differ among populations. Both pilfering and food hoarding behaviours allow animals to survive periods of food shortage, and are important for understanding how resources can influence the survival and fitness of individuals and populations.

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APPENDIX I

Pins used in the cone mark-recapture study. Each squirrel was assigned a unique colour combination. Colours used were: white (W), black (Bk), orange (O), red (R), green (G), blue (B) and yellow (Y). Pins were inserted into the rachis of the cone.

APPENDIX II

Results from the pin-search pilot study where a participant searched for 100 hidden pins for a minimum of 2 hours using a Garrett Ace 250 metal detector with a sniper coil.

Midden	**Painted?**	**Number Recovered**
1	Yes	75
2	No	61
3	No	41
4	Yes	78
5	Yes	63
Kluane Average	**-**	**63**
Gerhardt (2005)	**-**	**54**