BREEDING SETTLEMENT AND DISPERSAL IN A NORTHERN POPULATION OF AMERICAN KESTRELS

by

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Abstract

Birds should choose breeding sites that will maximize fitness. In so doing, they must evaluate a host of environmental and ecological cues that signal the costs and benefits that may be realized at a particular breeding site. This evaluation begins at a broad spatial scale, such as when deciding whether to undergo large among-year movements, and continues to the finest scale which involves an evaluation of the specific attributes of potential nest sites. Furthermore, parents should invest in reproduction to maximize their fitness according to the conditions existing at their breeding site. I evaluated the influence of prey abundance and structural features of the nest and surrounding habitat on nest-site selection, and reproductive investment and success of a population of American kestrels (*Falco sparverius*) in north-central Saskatchewan. I also evaluated the influence of the perception of the risk of nest predation on these variables by experimentally manipulating auditory and visual cues of the presence of a common nest predator near nest sites. Finally, I utilized stable hydrogen isotope ratios in feathers to examine among-year settlement decisions (breeding dispersal) and conducted preliminary analyses to ascertain the mechanisms responsible for the observed variation in hydrogen-isotope values in the feathers of kestrels.

Prey abundance did not influence nest-site selection but was negatively associated with the timing of clutch initiation. Kestrels preferentially chose nest boxes with unobstructed entrances and in recently harvested forests, and laid clutches of lower volume in forests with a heavier deciduous component. Mass of female nestlings was greater in boxes at the forest edge and on jack pine (*Pinus banksiana*), and feather lengths of males nestlings were greater in nests on trees in poor health. Experimentally increasing the perceived risk of nest predation did not affect nest-site selection, but induced kestrels to initiate breeding later in the season, and to lay larger clutches. To quantify breeding dispersal, I used known-origin birds to establish the expected local hydrogen-isotope ratios (δD) in feathers but found the δD in the feathers of these individuals to be substantially more a positive (deuterium enriched) than expected relative to long-term weighted-average values of precipitation or kestrel-specific GIS models of expected δD of feathers. In addition, I found significant age differences in δD values of feathers which complicated efforts to separate local from immigrant birds. To explore the cause of such enrichment I compared the δD of feathers and plasma of adult birds, and nestling feathers. I also examined how the degree of deuterium enrichment in adult feathers related to adult mass, structural size, and reproductive effort at the time of growth. I found adult feathers grown at my study area during breeding were significantly more deuterium enriched than plasma, and showed non-overlapping distributions with nestling feathers. Males that were structurally larger as well as females that fledged female nestlings of greater mass, and males whose mates laid clutches of lower volume, exhibited greater deuterium enrichment in their feathers.

My study showed that further examination of the processes affecting individual physiologies during breeding may lead to a better understanding of deuterium enrichment of raptor feathers. My study also highlights the complexity of the ecology of nest-site selection, suggesting that while food is important for certain aspects of reproduction, interspecific and scale-dependent interactions with landscape features play an important role in nest-site selection and breeding decisions.

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1. General Introduction

Understanding the constraints acting on the evolution of avian life-histories and population processes requires knowledge of the factors that influence avian movements, settlement, and interactions among populations (Walters 1998, 2000). Birds make decisions about movement and settlement at a number of scales. Within the year, individuals may undergo a post-natal dispersal, or migrate between breeding and wintering grounds. Post-natal dispersal distances are usually on the order of territories, but migration often involves travelling great distances (Rubenstein et al. 2002). Between years, individuals may settle in the same (philopatry) breeding or wintering location as in the previous year, or they may settle in a different location (dispersal) from the previous year (Clobert et al. 2001). Spatially, settlement occurs on a hierarchical scale; as the spatial scale becomes increasingly narrowed, it reflects the heterogeneity of the habitat at the spatial scale above it (Pribil and Picman 1997).

The evolution of dispersal and settlement strategies is influenced by a host of factors acting both individually and in concert. Inbreeding avoidance is the primary genetic explanation invoked to explain natal and breeding dispersal, and sex-biased dispersal may serve this purpose in some cases (Greenwood 1980, Pusey 1987, Negro et al. 1997, Restani and Mattox 2000). Inter- and intraspecific interactions will constrain both movement and settlement and the manner in which this occurs will depend on how these interactions vary in space and time (Negro et al. 1997, Robinson and Oring 1997, Clobert et al. 2001, Hoover 2003). The ultimate consequences of settlement decisions for fitness will depend on an individual's prior knowledge and subsequent realization of the local resource availability and deleterious threats such as predation, parasitism, and adverse weather (Greenwood 1980, Emlen 1991, Orians and Wittenberger 1991, Weatherhead and Forbes 1994, Hoover 2003).

Detecting the settlement and dispersal patterns of migratory birds is problematic, particularly at a broad scale. The vast distances involved in migration mean that most migratory birds are difficult to track, both within and between years (Chamberlain et al. 1997, Kelly and Finch 1998, Wassenaar and Hobson 2000, Hobson et. al 2004). Given that the causes and consequences of settlement decisions will vary geographically in accordance with local ecology and phenology, it is desirable to adopt a multifaceted approach to studying breeding settlement decisions. Such an approach may best identify how various factors interact to influence these decisions and their consequences for fitness (Clobert et al. 2001).

1.1 Study species and area

I studied American kestrels (*Falco sparverius*) at a location in the boreal forest of north-central Saskatchewan, near Besnard Lake (55°N, 106°W). The landscape in this area is comprised largely of coniferous trees such as white (*Picea glauca*) and black spruce (*P. mariana*), and jack pine (*Pinus banksiana*), but frequently includes a mix of deciduous trees such as trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). A large part of the study area was burned in a forest fire in 1995 (described in Dawson and Bortolotti 1999) and is now comprised of thick regeneration of mostly jack pine. There are numerous wetlands throughout the study area and it is subject to continual timber harvest for the pulp and paper industry; therefore, the landscape is a patchwork of variable-sized openings and seral stages.

American kestrels are small falcons that are widespread in North America. There are many recognized subspecies of kestrel (Smallwood and Bird 2002), and while some populations are year-round residents, many are migratory; those individuals that breed the furthest north also migrate furthest south, while individuals at intermediate latitudes undergo shorter migrations (Smallwood and Bird 2002). Kestrels are sexually dimorphic; males are smaller than females and there are distinct differences in plumage coloration between sexes. Breeding pairs are generally monogamous within breeding seasons, and are secondary cavity nesters, utilizing cavities excavated by various species of woodpecker as well as natural cavities (Balgooyen 1976). Kestrels will readily use nest boxes and as a result, have been the subject of extensive study (Bortolotti 1994). This species is found throughout North America in a variety of habitats. Generally they are found in landscapes with variable openings such as meadows or agricultural fields, but require trees for perching and nesting (Smallwood and Bird 2002). Although widespread, and the focus of numerous studies, relatively few data exist describing the correlates of breeding habitat selection (e.g. Rohrbaugh and Yahner 1997, Santolo and Yamamoto 2009, Smallwood and Collopy 2009, Smallwood et al. 2009b). Kestrels consume a wide variety of prey, including insects such as grasshoppers and dragonflies, frogs, small birds, and small mammals, but the most important food source varies geographically (Bortolotti et al. 2000, Smallwood and Bird 2002).

The study area contained a total of 222 nest boxes erected on aspen or jack pine trees, or on decommissioned power poles. These were situated along gravel roads, although the exact distance from the road varied. Boxes were, on average, 3.6 m above the ground, and box dimensions were 20.5 cm wide by 23.5 cm deep by 42.7 cm tall; the entrance holes were 7.5 cm in diameter. The roofs were slanted and lifted open to provide access to the birds inside.

During my study, box occupancy was 29% versus 44% and 33% in 1995 and 2003 respectively (Dawson and Bortolotti 2006). Similar declines in nest-box occupancy have been reported for numerous other study locations, and Breeding Bird Surveys indicate significant negative population trends for both Canada and the US (Smallwood et al. 2009a). The cause(s) of these declines are unknown, although Smallwood et al. (2009a) suggested potential causes may occur on wintering grounds or during migration. These authors also suggested that habitat quality did not seem to be the cause of declines at one study area based on the nesting success of those individuals that bred there. Nonetheless, this species nests in a broad range of landscapes, where the features that constitute a high-quality nest-site may vary based on, for example, the main prey sources, the prevalence and composition of parasites, or the type of predators present. Furthermore, breeding phenology varies by location as a function of the extent of migration that individuals undergo and so the relative influence of breeding habitat quality may likewise vary. Therefore, testing hypotheses about habitat quality and its importance for breeding success at a regional level appears important for revealing the causes of population decline in this species. In addition, if events or conditions encountered during wintering and migration are contributing to this decline, then describing within-and among-year movement (dispersal) will be necessary to quantify these effects.

1.2 Study objectives

The objective of this thesis was to utilize both experimental and comparative methods to examine how kestrels decide where to breed and the ensuing consequences for reproductive success. When selecting a breeding site, birds should choose a site that will result in the highest net fitness gain (Morris 2003). Site characteristics which may influence this net gain include environmental factors such as microclimate and weather conditions, and ecological interactions such as prey abundance and availability, risk of predation, and prevalence of parasites (Fontaine and Martin 2006a). The influence of these may also be mediated by the structure and composition of the surrounding habitat. In chapter 2, I present results of a study that examined nest-box selection and reproduction in relation to structural habitat features measured during the course of my field work. This study also used historical data collected at this site to examine nest-box selection and reproduction in relation to an index of prey abundance, measured at individual nest boxes, over eight years (1990-1997). Prey availability at this site is known to influence parental investment and behaviour (Wiebe and Bortolotti 1995, Dawson and Bortolotti 2002) and my study tests the hypothesis that nest sites associated with high prey abundance represent high-quality sites (Sergio and Newton 2003). I also examined whether adults adjust their reproductive decisions and realize differing success in response to these features.

The risk of nest predation is known to be an important constraint on reproductive success (Ricklefs 1969, Martin 1995, Thompson 2007). Studies have shown that birds can alter clutch size in response to predation risk (Lima 2009), but these results are equivocal in cavity nesting birds (Martin and Li 1992). Furthermore, nearly all studies examining the role of nest predation in limiting avian reproduction have focused on realized predation risk. In chapter 3, I present the results of an experiment that used playbacks of vocalizations of red squirrels (*Tamiasciurus hudsonicus*) to test whether kestrels will adjust nest-site selection, timing of breeding, and reproductive investment based on cues designed to represent the risk (perception) of nest predation.

Between-year dispersal from natal or breeding sites is difficult to follow if the movements are greater than several territories (Hobson et al. 2004) and it can be difficult to distinguish mortality from dispersal (Drilling and Thompson 1988, Waser et al.1994). Yet, this is necessary information for a meaningful understanding of source-sink and metapopulation dynamics (Hobson et al. 2004). Some studies have utilized stable-isotope methods to quantify breeding and natal dispersal (e.g. Hobson et al. 2004, Girvan et al. 2007, Studds et al. 2008, Wunder 2007, Coulton and Clark 2008). Isotopes of elements occur in varying forms which differ in the number of neutrons present in the nucleus (Hoefs 2004, Wassenaar 2008) and although chemically similar, different isotopes of the same element exhibit different rates of reaction depending on conditions (Hobson 2008). Hydrogen-isotope ratios are the ratio of heavy to light hydrogen ($^2H/^1H$, depicted as δD) present in atmospheric water and hence, local rainfall. The general pattern of δD in North American precipitation (δD_p) is one of decreasing enrichment from the southeast to northwest, low to high altitudes, coastal to inland areas, and warm to cool climates (Dansgaard 1964, Hobson 2011). This depletion occurs due to a combination of spatial and temporal processes which result in the cumulative loss of the heavier isotope as it rains out of moist air masses (Meehan et al. 2004, Hobson 2011). These δD_p patterns are reflected in the tissues of consumers (Chamberlain et al. 1997, Hobson and Wassenaar 1997). If the tissue is inert after growth, as is the case with feathers, and if the timing of growth is known, an individual can be sampled at any time and its origins at the time of growth inferred from the δD in those tissues. If the tissue is metabolically dynamic, inferences can be made about the location of the individual at a given time when the isotopic turnover rate of the tissue is known. In chapter 4, I present results from a study which utilized stable-hydrogen isotopes in the feathers of kestrels to describe and quantify the extent of breeding and natal dispersal in this population. I sampled feathers, which are grown once per year, during breeding, in an attempt to determine the location that each individual bred in or hatched from in the previous year. I found the hydrogen isotope ratios in feathers of kestrels of known origin were substantially more deuterium enriched relative to rainfall than nestling feathers and other avian species. This, in addition to the inability to accurately age unknown individuals, complicated the use of this tool to determine the provenance of kestrels of unknown origin. Consequently, I conducted preliminary analyses which focused on identifying potential relationships between characteristics of individual birds or their reproduction which may influence their physiologies and the δD in feathers.

2. Nest- and territory-scale predictors of nest-site selection, and reproductive investment and success in a northern population of American kestrels (*Falco sparverius*).

2.1 Abstract

In a heterogeneous landscape, birds must evaluate environmental cues that signal the fitness benefits to be gained from a breeding site. Little study has been devoted to the factors that influence settlement decisions and their implications for breeding in northern populations of American kestrels. I examined nest-site selection and reproductive investment and success of this species in relation to the abundance of small mammals from 1990 to 1997, and territory and nest-site attributes in 2008. Nest-site selection was not associated with prey abundance; however, females initiated laying earlier on territories with higher prey abundance. Kestrels were more likely to choose nest boxes with unobstructed entrances and in recently harvested forests, and laid clutches of lower volume in forests with a heavier deciduous component. Nestling mass (females) was greater in boxes at the forest edge and on jack pine, and feather lengths (males) were greater in nests on trees in poor health. I discuss the importance of these features for provisioning and nest vigilance and propose that kestrels in my area make decisions based on interactions occurring at scales intermediate to the landscape and territory levels.

2.2 Introduction

Upon return from southern wintering grounds, migratory birds make a series of decisions which culminate in the selection of a nest site in which to breed. Breeding-site selection occurs on a hierarchical scale (Pribil and Picma, 1997); an individual chooses the general landscape, and then decides how it will utilize patches within that landscape, and objects within those patches (Orians and Wittenberger 1991). There may be costs associated with resource limitation, competition, sub-optimal weather, and predation risk, and the choice of breeding habitat should minimize the costs associated with these (Fontaine and Martin 2006a). Specific attributes of breeding sites may serve as direct or indirect cues for prospecting birds to assess the net fitness gain associated with a site; they may signal the prevalence of predators, which are important drivers of nest failure (Martin 1995) and productivity (Thompson 2007), or parasites, which can be detrimental to nestling growth (Nilsson et al. 2003) and adult survival (Brown et al. 1995). Breeding-site characteristics may also influence nest and ambient microclimate which can affect egg investment and viability (Webb 1987), incubation behaviour (Wiebe and Martin 1997), hatching asynchrony (Ardia et al. 2009), nestling growth and survival (Dawson et al. 2005), and parental energy requirements (Ardia et al. 2009).

In many avian species, prey availability has been linked to a host of reproductive variables. For example, among two species of small falcon, American kestrels (*Falco sparverius*, hereafter, "kestrels") and Eurasian kestrels (*F. tinnunculus*), prey availability can affect hatching asynchrony (Wiebe and Bortolotti 1994), sex allocation (Martinez-Padilla and Fargallo 2007), egg size (Wiebe and Bortolotti 1994, 1995), and nestling size and survival (Dawson and Bortolotti 2000a); breeding settlement in Eurasian kestrels also is highly correlated with prey abundance at the landscape scale (Kormipäki 1994), but it is unknown whether American kestrels show similar patterns at any scale and if so, how they evaluate prey abundance.

In North America, kestrels are widespread; however, the features that influence breeding-site selection of this species have been studied primarily in populations breeding in central and southern latitudes (e.g. Smallwood et al. 2009b). The composition and availability of breeding habitat varies widely among study areas and in northern areas of their breeding range, very little is known about how kestrels decide where to breed, and how these decisions influence fitness. Recent estimates indicate significant declines in populations throughout portions of North America (Farmer and Smith 2009). The reasons for these declines remain unclear (Smallwood et al. 2009a). The choice of breeding location has important fitness consequences for individuals (Cody 1985), and the extensive range of this species means that the ecological interactions they contend with during breeding, and the subsequent implications for fitness, probably vary geographically. It is therefore necessary to assess the factors that affect breeding-site selection at multiple scales and locations throughout the breeding range, which may identify some of the mechanisms behind geographic variation in life histories, and changes in population status. To address this need, I studied a population of kestrels that breed in the boreal forest in north-central Saskatchewan to evaluate the territory and nest-site features that I hypothesized may be important predictors of nest-site selection, and reproductive investment and success. I also tested whether prey abundance predicted nest-site selection and reproductive investment and success over an eight year time span.

2.3 Methods

2.3.1 Study area

I studied American kestrels utilizing nest boxes in the boreal forest near Besnard Lake, Saskatchewan (55°N, 106°W). The study area is comprised of a network of nest boxes generally situated along gravel roads. Forest composition near Besnard Lake is a combination of deciduous and hardwood, and active logging and reforestation occur regularly; for detailed descriptions of the site refer to Gerrard et al. (1996). A portion of the study area was burned in a large forest fire in 1995 that killed the majority of the trees (Dawson and Bortolotti 1999) and this area is now composed primarily of dense jack pine (*Pinus banksiana*) regeneration. Data were collected to determine nest-site features associated with nest-box selection, re-use, reproductive investment, and success in 2008. This nest-box population of kestrels has been studied since 1988 and I used data from 1990 to 1997 to evaluate the role of prey abundance on these same outcomes.

2.3.2 Field Techniques

2.3.2.1 Nest-site features

For 222 nest boxes, I evaluated 10 features associated with the immediate area surrounding the nest-box tree, the tree that the nest box was mounted on, and the nest box itself (described in Table 2.1). The surrounding composition category "mature" encompassed mature, primarily conifer stands. These had not been subjected to recent disturbance but were often comprised of old jack pine plantations, with little undergrowth. "Recently harvested" were cut blocks with no regeneration, and "Regenerating" were cut blocks with jack pine plantations lower than the height of the

Table 2.1. List of nest-site variables classified in the vicinity of nest-boxes available for American kestrels.

Variable Name	Description	Categories
Surrounding Composition	Forest composition immediately surrounding nest-box tree	Mature, Recently harvested, Regenerating, Burn, Deciduous disturbed
Tree Species	Species of tree on which nest-box was mounted	Jack Pine, Aspen
Tree Health	Health status of nest-box tree	Live/healthy, live/unhealthy, dead
D to E	Distance of nest-box tree from forest edge	0m (edge), > 0m (away from edge)
Orientation	Spatial orientation of nest box entrance hole	N (316°- 44°), E (46° - 135°), S (136° - 225°), W (226° - 315°)
Chewed	Incisor marks around entrance holes resulting from chewing by red squirrels	Yes, No
Entrance Obstruction	Degree of entrance obstruction	Clear, Obstructed
DBH	Tree diameter at breast height	Continuous
DCH	Tree diameter at cavity height	Continuous
Box Height	Height of box placement on tree	Continuous

boxes (approximately 3.6 m high on average). "Deciduous disturbed" were comprised of mixed deciduous species, with a heavy aspen (*Populus tremuloides*) component, variable openings from blow down and other sources of disturbance, and a significant under-story component. In the "burned" portion of the study area, all boxes were mounted on decommissioned utility poles near the road edge with no cover or entrance obstruction; the jack pine regeneration in the burn was in all cases below the height of the nest box. For tree health, "live/healthy" trees were comprised of all live branches, "live/unhealthy" trees had both live and dead branches, and "dead" trees consisted of all dead branches or were snags. I classified nest-box entrances as obstructed if any sort of vegetative (branch, leaves, etc.) structure obstructed the area around the entrance hole from any angle. Diameter at breast (DBH) and cavity height (DCH) were measured using a DBH measuring tape, with DCH measured at the top edge of the nest boxes; box height was measured from the bottom of the box to the ground. I assessed nest-site features at the completion of breeding in 2007 to avoid disturbance to active nests, and re-assessed each box for changes before and after breeding in 2008. I did not include nest use and reproduction from 2007 due to an experiment conducted in that year which adversely affected nest-box selection.

Starting in early May 2008, I visited nest boxes every three to five days to determine clutch initiation dates in those boxes where eggs were laid; these are referred to as "selected" boxes. Upon clutch completion, I returned to determine clutch size, measure eggs, and capture adults. I measured the length (l) and breadth (b) of each egg, and for adults I measured length of tarsus, culmen, 10th primary feather, central and outer rectrices, and unflattened wing chord, and recorded mass. Mass was measured to the nearest gram with a spring balance, feather lengths to the nearest 0.5mm with a ruler, while all other measurements were to the nearest 0.1mm with digital calipers. Clutch volume was calculated by summing the volume of each egg in the nest, estimated using the equation $0.51*l*b^2$ (Hoyt 1979). I examined total clutch volume because American kestrels have been shown to increase egg size rather than clutch size in response to increased food, suggesting that this species may favor higher offspring quality rather than risking the demands of raising additional offspring when resources are abundant (Wiebe and Bortolotti 1995). I examined adult condition to determine whether attributes of nest-sites were likely to result in their selection by lower or higher quality individuals. To obtain an index of adult condition, I first input the six linear size measurements taken from all adults (first capture only) caught on the study area in 2007 and 2008 into a principal components analysis (PCA); males and females were analyzed separately (Bortolotti and Iko 1992). As an index of body condition for males, I removed the effect of body size on mass by using the residuals from a linear regression of body mass, measured during incubation, on the first component (PC1; n = 130, 49.89% variance explained; Dawson and Bortolotti 2000b). The condition of kestrels can vary during the breeding season (Dawson and Bortolotti 1997); however, I detected no relationship between capture date and condition so did not correct for capture date. There was no relationship between PC1 (n = 105, 48.30% variance explained) and female mass, measured during incubation, (r = 0.01, P = 0.90, n = 99) among females in my study area in 2008, so I used mass as a proxy for body condition.

Active nests were visited every day, starting 29 days after the third egg was laid, to determine hatching date; nestling age was assigned based on the age of the first-hatched nestling. I visited nests every four to five days throughout the brood-rearing period to monitor nestling growth and mortality. When nestlings were 24 days old I recorded the mass, and the length of the 10^{th} primary of each nestling. Kestrels exhibit sexual dimorphism; male and female plumage can be differentiated by 13 days of age, and size differences are also evident by this time (Anderson et al. 1993). I therefore calculated the mean mass and length of 10^{th} primary of nestlings in each nest at day 24 for males and females separately. Kestrels fledge between 24 and 30 days of age; I did not visit nests after 24 days of age and considered nestlings to have fledged if they were present in the nest at day 24, and were not found dead in the box at the end of the season.

2.3.2.2 Prey abundance

To quantify prey abundance, small mammal censuses were conducted in the vicinity of the same 33 nest boxes each year, between 1990 and 1997. Trapping took place for a period of three days and nights in both early May and early July. May is the time when kestrels are establishing territories, pair bonds, and nests, and when females are acquiring nutrients for egg production. July is the peak period for nestling provisioning. Trap lines were set 100m from each nest box and consisted of 10 stations spaced 30 m apart and situated 10 m from and parallel to the road. Two snap traps were placed at each station and baited with peanut butter. Traps were checked and reset each morning for three days (Wiebe and Bortolotti 1992). For both the May and July trapping periods, I standardized each three-night trapping session to the mean number of voles and small mammals per 100 trap nights. Although kestrels feed on a variety of small mammal species, the primary prey species in my area is the southern red-backed vole

(*Clethrionomys gapperi*; Bortolotti et al. 2000). To facilitate an evaluation of the relative importance of vole species versus other small mammals, I calculated this index for all vole species and all other small mammal species separately. Similar protocols were followed in 1990-97 as described above to determine selection of nest-boxes, clutch initiation dates, clutch size, and the number of young fledged at each box.

2.3.3 Data analyses

2.3.3.1 Nest-site features

To assess the influence of nest-site features on nest-box selection in 2008, I used logistic regression, with a binary response variable (selected, not selected). I assessed model fit of binary logistic models using the likelihood-ratio test and assessed each variable by the loss of model fit that occurred with the exclusion of each variable; I also assessed each variable with the Wald statistic (Quinn and Keough 2002). Overall model fit and individual variables were evaluated with the deviance chi-square statistic (G^2; Quinn and Keough 2002). Variables that did not improve model fit ($P > 0.05$) were sequentially removed beginning with the variable with the lowest G^2, until each remaining variable significantly improved model fit. The effect of each variable in the final models was again assessed based on the likelihood ratio test of the reduced model and the Wald statistic, and I employed the odds ratio to describe how the odds of a nest-box being selected changed among levels of each independent variable. I used General Linear Models (GLM), with the continuous response variables being either adult male condition or adult female mass, to determine whether adults in better or worse condition secured nest boxes associated with certain nest-site features.

To determine the effect of nest-site variables on reproduction in boxes that were selected, I examined clutch initiation date, clutch volume, productivity (number of young fledged/nest), and mean mass and length of 10th primary of male and female nestlings in each nest at day 24. I did not include whether the entrance hole was chewed as an independent variable in these analyses because some box entrance holes were experimentally altered to mimic their being "chewed" by red squirrels (*Tamiasciurus hudsonicus*; described below). I would therefore be unable to determine whether significant effects were due to the presence of squirrels, or parental differences in nest selection. For nestling variables, I excluded one nest containing only a single nestling which routinely had an unusually full crop during visits, and whose measurements had a disproportionate influence on the distribution of the data. The relationships between nest-site features and clutch volume, nestling mass, and length of 10th primary were assessed using GLM and because factors such as the timing of clutch initiation or the condition of either parent may influence breeding outcomes, I included these as covariates. I examined preliminary models and sequentially removed fixed factors, interaction terms, and covariates that did not approach significance ($P > 0.10$), beginning with the lowest F-values.

In 2008, I conducted an experiment at some nest boxes which used playbacks of vocalizations of red squirrels, the main nest predators of kestrels, and chiselled nest-box entrance holes to simulate the risk of nest predation (Chapter 3). I examined nest-site selection and reproductive investment in relation to this experiment. Whether or not a box was a part of this experiment significantly affected both fledging success and length of 10th primaries of male nestlings (Greenwood and Dawson, *unpubl. data*); however, this was not independent of the other variable(s) selected for entry in to the preliminary models. For these analyses of fledging success and length of 10th primaries of male nestlings, I therefore used Linear Mixed Models (LMM) with maximum likelihood estimation, to account for the non-independence of observations from experimental boxes that were associated with the other relevant nest-site feature(s); experiment was included as a random factor in these cases.

For each set of analyses (both binary and linear response variables), I began by assembling preliminary models using an entry criteria of $P < 0.25$ (Hosmer and Lemeshow 2000) for independent variables based on univariate analyses of each measured variable against the response using G-tests, Analysis of Variance (ANOVA), or t-tests. The independent variables that I measured to describe nest-site features were chosen based on a general knowledge of the breeding behaviour of kestrels in my study area, and I included an additional variable to account for the potential influence of the experiment I describe above. For both binary and linear response variables, if no predictor variables reached model entry criteria of $P < 0.25$ I interpreted this as an indication that none of the variables I examined influenced the dependent variable of interest in 2008.

I also used contingency tables to test for independence among candidate predictor variables. Preliminary analyses showed that surrounding composition was often interdependent with a number of the other predictor variables. This relationship appeared substantially driven by boxes located in the burned area as each of these boxes held a similar profile of nest-site features. I therefore excluded boxes located in the burn from each analysis and ran separate tests to examine differences in each response variable between boxes located in the burn, and boxes located in all other classes of surrounding composition. In other instances of non-independence I included only surrounding composition, because it was frequently related to and appeared to represent variation in multiple other independent variables. The exception to this was in the analysis of the number of young fledged, where surrounding composition violated the assumption of equality of variances (Quinn and Keough 2002) and transformations failed to correct this; I therefore chose to use the other variable that met entry criteria, tree health, in this instance rather than surrounding composition.

2.3.3.2 Prey abundance

To evaluate whether overall prey abundance differed among years, I conducted a repeated-measures ANOVA with year as the repeated measure, and the number of voles and other small mammals/100 trap nights as the response variable; separate analyses were conducted for May and July. The assumption of sphericity of the covariance matrices was violated in the analyses of the number of voles for May and July, and for the number of other small mammals in July. This type of violation can increase Type I error, so I used the more conservative Greenhouse-Geisser adjustments of Epsilon and degrees of freedom were corrected accordingly (Quinn and Keough 2002).

My prey indices were quantified in the vicinity of a discrete set of nest-boxes (n = 33) in eight successive years; to account for the non-independence of these observations, I used Generalized Estimating Equations (GEE), which are an extension of generalized linear models (Liang and Zeger 1986). These use correlation matrices to estimate the covariance structure of correlated or interdependent explanatory variables (Paradis and

Claude 2002). I used GEE to test for a significant influence of prey abundance on nest-box selection, clutch initiation date, clutch size, and productivity (the number of young fledged/nest). Here I used clutch size rather than volume because I did not have egg measurements to calculate volume for all eight years. In all cases, year was the repeated measure, and the number of voles and other small mammals/100 trap nights were scale predictors. For nest-box selection, clutch initiation date, and clutch size, I used prey indices from May as predictor variables, and for productivity I used prey indices from July as predictor variables. To assess the influence of prey abundance on nest-box selection, I used a binary logistic model with logit link; for clutch initiation date, clutch size, and productivity, I used a linear model with an identity link function. In all cases I used a deviance scale, an exchangeable working correlation matrix, and estimated the covariance matrix with the robust estimator (Hosmer and Lemeshow 2000). In addition to using a repeated measure to incorporate the non-independence of data for each box over time, I initially included year as a fixed factor in all models to examine annual effects. I also included clutch initiation date as a covariate in my analyses of reproductive variables. I used a backwards stepwise approach, removing covariates at $P > 0.10$. To assess whether the average prey abundance in the vicinity of nest boxes over time affected the degree to which boxes are repeatedly selected, I performed a correlation analysis of mean number of voles and other small mammals/100 trap nights/year for each of May and July in relation to the proportion of years in which each box was chosen.

Statistical analyses were performed with SPSS 16.0 (SPSS Inc., Somers, New York, USA) and I considered results significant at $P = 0.05$. All means are shown ± 1SE.

2.4 Results

2.4.1 Nest-site features

In 2008, kestrels laid at least one egg in 64 of 222 nest boxes; 17 (out of 27) of these were located in the burned area. Boxes in the burned area were 4.8 times more likely to be selected than boxes in all other habitat composition types ($\beta = 1.57$, SE = 0.42, Wald = 13.84, df = 1, $P < 0.001$). Excluding boxes located in the burn, the final logistic model that predicted nest-box selection in 2008 ($G^2 = 20.04$, df = 4, $P < 0.001$) included surrounding composition ($G^2_{\text{reduced}} = 8.32$, df = 3, $P = 0.04$; Fig. 2.1a) and entrance obstruction ($G^2_{\text{reduced}} = 9.56$, df = 1, $P = 0.002$; Fig 2.1b); no interaction terms improved model fit. Distance to edge and tree species also met model entry criteria but were interdependent with surrounding composition so were not included. Boxes with an unobstructed entrance hole were 3.2 times more likely to be selected than boxes with obstructed entrance holes ($\beta = 1.16$, SE = 0.25, Wald = 21.79, $P < 0.001$). Boxes located in surrounding composition type "mature" were 87% less likely to be selected than those in "recently harvested" ($\beta = -2.03$, SE = 0.47, Wald = 18.56, $P < 0.001$); the odds of "deciduous disturbed" boxes being selected were 82% less than "recently harvested" ($\beta = -1.73$, SE = 0.52, Wald = 12.79, $P < 0.001$) and those of "regenerating" being selected were 85% lower than "recently harvested" ($\beta = -1.89$, SE = 0.53, Wald = 10.97, $P = 0.001$; Fig. 2.1).

Neither male condition nor female mass was associated with the nest-site variables that I examined. The exception was that males nesting in the burned area were in better condition during incubation by a mean residual mass of 6.85 g than those nesting

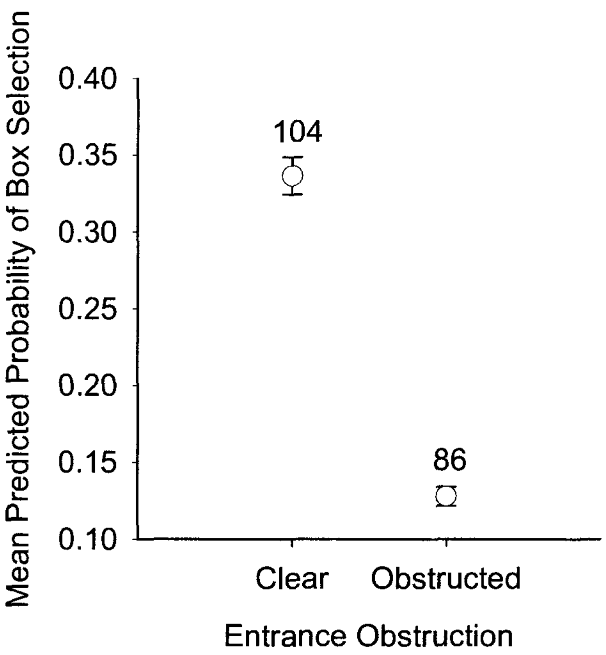

Figure 2.1a. Mean predicted probabilities (±1SE) from logistic regression of nest-box selection by American kestrels and degree of entrance obstruction.

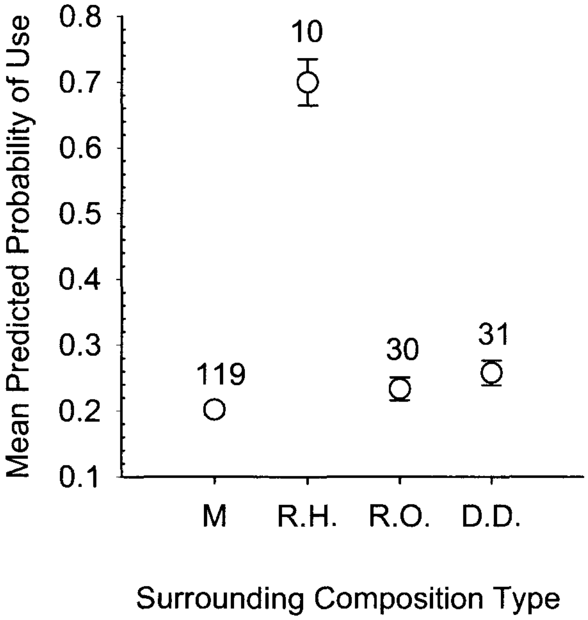

Figure 2.1b. Mean predicted probabilities (±1SE) from logistic regression of nest-box selection by American kestrels and surrounding composition type. Surrounding composition types are abbreviated as: M (mature), R.H. (recently harvested), R.O. (regenerating, old), and D.D. (deciduous disturbed).

elsewhere ($t = 3.18$, df = 42, $P = 0.003$). Although females nesting in the burn were on average 2.93 g heavier, this difference was not significant ($t = 1.02$, df = 55, $P = 0.31$).

2.4.2 Reproductive investment and success

No nest-site variables satisfied entry criteria for clutch initiation date, and the timing of clutch initiation did not differ between boxes in the burned area and all other boxes ($t = 0.96$, df = 56, $P = 0.34$). The final model for clutch volume included clutch initiation date as a covariate, but surrounding composition was the only nest-site feature, so I included boxes located in the burn for this analyses. Clutch volume significantly declined with later clutch initiation ($F_{1,51} = 10.51$, $P < 0.01$), and the surrounding composition that a box was located in also significantly influenced clutch volume ($F_{4,51} = 4.73$, $P < 0.01$). This relationship was largely driven by the clutch volume of nests in boxes located in deciduous disturbed areas; Bonferroni-adjusted comparisons showed clutch volume in these boxes was significantly lower than in those located in "mature" ($P < 0.01$), "regenerating" ($P = 0.04$), and "burned" ($P = 0.03$), but not "recently harvested" habitats ($P = 0.13$; Fig. 2.2).

Tree health was the only variable that met model entry criteria for determinants of productivity but did not show a significant influence on the number of young fledged when experimental status was accounted for as a random factor ($\mathrm{F}_{2,\,26\,62} = 2.99$, $P = 0.07$; marginal means: healthy = 3.03± 0.42, unhealthy = 1.99 ± 0.39, dead = 3.91± 0.92). The mass of the female parent was also positively related to the number of young fledged ($F_{1,37\,37} = 5.52$, $P = 0.02$). The number of young fledged in boxes located in the burn was not different from all other surrounding composition types (t-test corrected for unequal

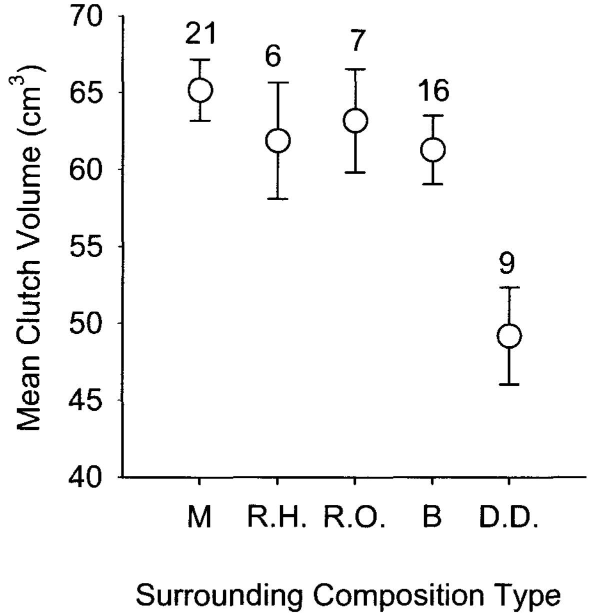

Figure 2.2 Marginal means (±1SE) of clutch volumes for pairs of American kestrels that nested in forests of different surrounding compositions. Surrounding composition types are abbreviated as: M (mature), R.H. (recently harvested), R.O. (regenerating, old), B (burned) and D.D. (deciduous disturbed). Bonferroni-adjusted comparisons showed mean clutch volume in "deciduous disturbed" areas to be significantly lower than "mature", "regenerating", and "burned", but not "recently harvested".

variances: $t = 1.80$, df = 33.82, $P = 0.08$). Although tree health and whether or not the box was located in the burn were not statistically significant at the $P \leq 0.05$ level, their close proximity to this limit may suggest some biological significance for productivity.

The only variable that met entry criteria in the analysis of nest-features on the mass of male nestlings at day 24 was entrance obstruction; male nestlings in nest boxes with clear entrances were heavier (clear = 110.12 ± 1.58 g, obstructed = 103.70 ± 4.48 g), but this result only approached statistical significance ($t = 1.89$, df = 35, $P = 0.07$). The final model examining nest-site features and mass of female nestlings at day 24 showed relationships with both distance to edge and tree species; there were no random factors or covariates in this model. The mass of nestling females was a mean of 8.60 ± 3.59 g higher in boxes located directly at the forest edge (0m) than those away from the edge (> 0 m; $F_{1,18} = 5.75$, $P = 0.03$) and 10.10 ± 4.17 g higher in nest-boxes on jack pine rather than aspen trees ($F_{1,18} = 5.87$ $P = 0.03$). There was no difference in mass of nestling females between boxes located in the burn and those located in all other surrounding composition types ($t = -0.20$, df = 31, $P = 0.85$). To determine if nest-site features influenced the length of 10^{th} primary of nestling males at day 24, I used a LMM; the final model included experiment as a random factor because it showed a marginal influence on the length of 10^{th} primaries of nestling males ($P = 0.06$) and tree health as a fixed factor. There was a significant main effect of tree health ($F_{2,24} = 4.80$, $P = 0.02$); Bonferroni-adjusted comparisons showed a significant difference between the feathers of males raised in boxes on live (60.85 ± 1.00 mm) and unhealthy trees (65.15 ± 1.09 mm); those on dead trees (65.50 ± 2.44 mm) were not different from either of the other two categories. No nest-site variables were significantly related to mean length of 10^{th} primary of female nestlings.

2.4.3 Prey abundance

Mean number of voles/100 trap nights was significantly different among years for both May ($F_{3\,47,111\,07} = 10.97$, $P < 0.001$), and July ($F_{4\,46,\,142\,80} = 10.82$, $P < 0.001$); the mean number of other small mammals was also significantly different among years for May ($F_{7,224} = 2.89$, $P < 0.01$) and July ($F_{4\,58,\,146\,50} = 14.68$, $P < 0.001$; Fig. 2.3).

Nest-box selection was not predicted by either the number of voles or other small mammals in May (Table 2.2). Clutch initiation dates were significantly earlier where both vole and all other mammal indices were higher; for each additional vole per 100 trap nights, females laid their first egg 0.42 days earlier and for each additional other mammal, females laid 0.24 days earlier (Table 2.2, Fig. 2.4). Clutch sizes were not significantly influenced by the number of voles/100 trap nights, but were positively related to the number of other small mammals/100 trap nights at a level approaching significance ($P = 0.06$; Table 2.2). Neither prey index significantly influenced overall productivity (Table 2.2).

The proportion of years in which a box was selected was not significantly correlated to the mean vole or other small mammal index (averaged across eight years) for either May or July (in all cases, $-0.15 \leq r \leq 0.15$, $P \geq 0.39$, $n = 33$).

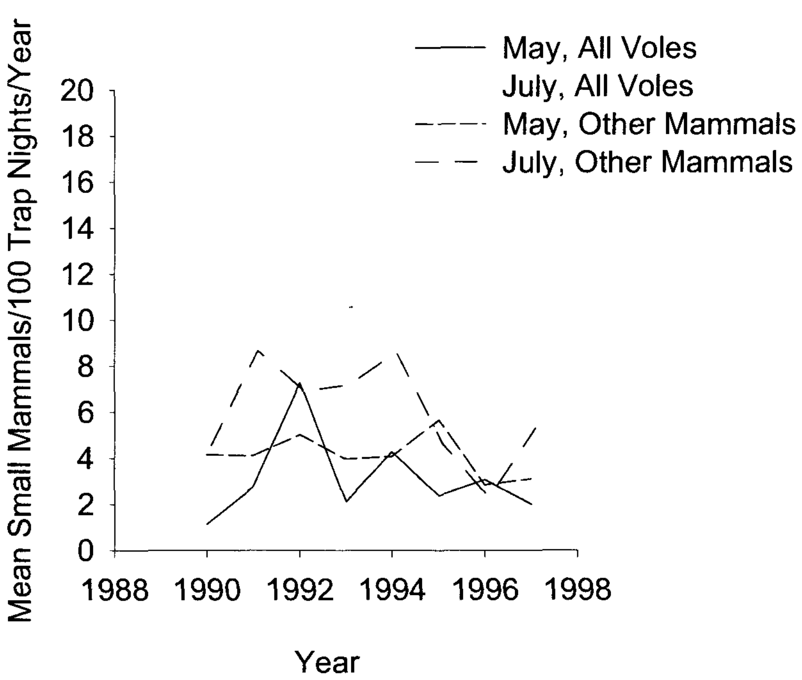

Figure 2.3 Annual means (per 100 trap nights) of voles, and all other small mammals censused in the vicinity of the same 33 nest boxes in May and July of each year, 1990-1997.

Table 2.2. Wald statistics and parameter estimates of models examining the effect of small mammal abundance on nest-box selection and reproduction of American kestrels. Odds ratios and 95% confidence intervals are given for the model (nest-box selection) with a binomial error distribution.

Dependent Variable	**Independent Variables/Covariates**	***Z***	**df**	***P***	**β**	**SE**	**Odds Ratio**	**95% Confidence Interval**
Nest Box Selection (yes/no)	Voles/100 trap nights in May	2.58	1	0.11	0.03	0.02	1.03	0.99 - 1.08
	All other small mammals/100 trap nights in May	0.20	1	0.65	-0.02	0.03	0.99	0.93 - 1.05
Julian Clutch Initiation Date	Voles/100 trap nights in May	17.55	1	0.00	-0.42	0.10		
	All other small mammals/100 trap nights in May	5.24	1	0.02	-0.24	0.11		
Clutch Size	Voles/100 trap nights in May	2.65	1	0.10	0.02	0.01		
	All other small mammals/100 trap nights in May	3.67	1	0.06	0.03	0.02		
Number of Young Fledged	Voles/100 trap nights in July	0.17	1	0.68	0.01	0.02		
	All other small mammals/100 trap nights in July	0.01	1	0.90	<-0.01	0.03		
	Clutch Initiation Date	4.45	1	0.04	-0.05	0.02		
	Year	18.12	7	0.01				

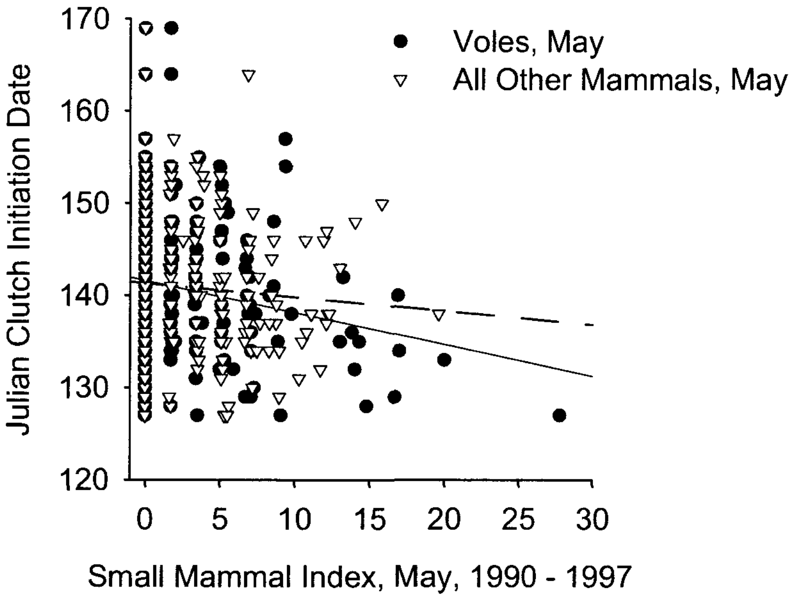

Figure 2.4 Julian clutch initiation dates of American kestrels in 33 nest boxes in the years 1990 – 1997 as a function of all voles and all other small mammals censused in the vicinity of each box in May.

2.5 Discussion

2.5.1 Breeding-site selection

I measured breeding site variables at both the territory, and nest-site scales. My results support the idea that more mature areas of the landscape are less suitable for kestrels to breed in. Boxes in mature, regenerating old, and deciduous disturbed forest types were between 82 and 87 % less likely to be chosen than boxes in recently harvested areas. Red-backed voles may increase in abundance the first year following harvest but tend to decrease in abundance during the next 10 years following harvest, whereas the abundance of deer mice (*Peromyscus maniculatus*) increases during this time (Fisher and Wilkinson 2005); this relationship is more pronounced following fire (Zwolak 2009). In both types of disturbance, the dynamic begins to shift 11 to 20 years after harvest when red-backed voles begin to dominate; the relative abundance of small mammals varies depending on site-specifics but red-backed voles are generally the most abundant in mature stands (Fisher and Wilkinson 2005). So, although the species composition may shift, prey abundance in harvested areas may be adequate to support successful reproduction. Kestrels hunt visually from perches or by hovering; harvested areas with snags or standing aspen therefore provide both perches and open landscapes in which to detect and capture prey. Although kestrels are widespread and nest in a variety of habitats, including agricultural land, forests, and deserts (Smallwood and Bird 2002), studies in other areas have also found nest box occupancy to be positively associated with more open canopy, lower ground cover, and less woody debris (Smallwood and Collopy 2009, Smallwood et al. 2009b, Bohall-Wood and Collopy 1986). Given the preference for more open breeding sites, I would have predicted that in addition to the recently harvested areas, deciduous disturbed habitats would have a high probability of being selected; however, the more substantial under-story component in these areas likely inhibits the ability to successfully detect and capture small mammals, the main prey in my study area (Bortolotti et al. 2000).

In addition to the ease of hunting, the risk of predation may vary in different surrounding composition types. In another study that I performed in 2008, I conducted transect surveys and found a mean abundance index of squirrels was the highest in the mature category and lowest in the deciduous disturbed (Greenwood and Dawson, *unpubl. data*). This provides anecdotal evidence that the more mature and coniferous areas may support greater numbers of squirrels. In that study, I found that nest-box selection is negatively influenced by the abundance of red squirrels (Chapter 3). Open habitats, especially clear-cuts, are unsuitable for red squirrels which are associated with mature conifer stands and large spruce, hardwood, and snag trees within these stands (Fisher and Wilkinson 2005, Fisher and Bradley 2006) so kestrels may be selecting boxes in more disturbed areas as a predator avoidance strategy.

This nest-box population has been declining over time; Dawson and Bortolotti (2006) found that nest box occupancy as of 2003 had remained constant in the area that was burned but had declined in all other stand types. These authors suggested that as the areas outside of the burn continue to mature, they become less suitable for kestrels, and that in the years following the fire, red squirrels may have been less abundant in the burned area. I found boxes in the burned area were almost five times more likely to be chosen than all other boxes, a clear indication that territory- and landscape-scale habitat features factor in to the decisions of kestrels concerning where to breed. Between 2007 and 2009, squirrels were commonly seen and heard in the burn, and active nests of squirrels were found in my boxes so anecdotal observations suggest that the burn is becoming more suitable for squirrels, but the threat of these nest predators may still be lower than in the mature forests. The costs to reproduction associated with nest predators (Martin 1995) would certainly warrant further examination of the use of the burned habitat by squirrels.

At the nest-site scale, unobstructed entrance holes were, on average, 3.2 times more likely to be chosen than those with vegetation obstructing the entrance. Although vegetation covering the nest hole may offer some protective concealment, it also allows greater lateral access to the nest for egg predators such as squirrels, mice, and other small mammals. Unobstructed entrances also provide adults with a clear path in to the box, which would be advantageous when the provisioning of nestlings requires frequent nest visits. Finally, before vacating the nest box upon disturbance, adults often peer out of the hole to first survey for threats before exiting; a clear entrance path provides the opportunity to be vigilant, assess imminent threats, and make an unobstructed escape.

Surprisingly, among the 33 boxes that were sampled over an eight year period, I found no correlation between small mammal abundance and nest box occupancy. A long-term monitoring program in Pennsylvania found that 25 % of nest boxes were occupied more often than would be expected if the frequency of box use was random, and the majority of fledglings were produced at a minority of boxes, suggesting either individual- or habitat-related quality differences between these and other boxes (Katzner et al. 2005). Similarly, I have observed that although occupancy rates may shift as the landscape changes, certain nest boxes are repeatedly used, year after year. I anticipated that this was a function of superior breeding-site quality, likely due to consistently favorable prey availability in the vicinity of those boxes through time; however, despite evidence that prey abundance influences egg size, hatching asynchrony, sex ratio, brood reduction, and parental provisioning behaviour (Wiebe and Bortolotti 1994, 1995, Dawson and Bortolotti, 2000a), all of which are important components of reproductive success, boxes associated with higher prey indices did not have correspondingly high occupancy. The breeding home-ranges of kestrels have been reported to be up to 194 ha in size (Craighead and Craighead 1956) and in north western New Jersey, occupancy rates were found to be highest in large contiguous patches of suitable habitat, lowest in small patches, and dependent on kestrel abundance in intermediate patches (Smallwood et al. 2009b). This suggests that although kestrels establish and defend breeding territories, the suitability of the landscape surrounding these territories is important, and influences settlement. Furthermore, Eurasian kestrels are known to closely track cyclical prey abundance at the landscape level in both space and time (Korpimäki 1994). It may therefore be necessary to examine prey availability over a larger area to describe the manner in which American kestrels appraise and utilize the landscape surrounding the nest site. The relative benefits of one breeding site over another may depend on the attributes of a larger patch, such that adequate nest sites with low local prey abundance may be chosen if there are portions of the territory or peripheral landscape with higher prey abundance and accessibility.

The only association I found between settlement and adult characteristics was that males that bred in boxes located in the burn were in better body condition during incubation. Upon formation of a pair-bond, the energy demands on male kestrels are high; between this time and the early brood-rearing period when the female resumes hunting, the male supplies the majority of the food for the female and young nestlings (Balgooyen 1976). Wiebe and Bortolotti (1992) found that males were more successful at maintaining body condition between arrival and laying in years where natural small mammal abundance was higher. I did not quantify prey in the burn during 2008, but the enhanced condition of males in this area could be a function of greater prey availability there. In addition, if the quality of the habitat in the burn is currently more suitable for breeding than that outside of the burn, higher quality males that are better equipped to maintain condition may be outcompeting lower quality males for these territories and nest boxes. Although I might expect a similar result among females, the mass and condition of this sex is difficult to assess unless all are measured at precisely the same time relative to egg-laying due to mass fluctuations as a function of egg production (Wiebe and Bortolotti 1992).

2.5.2 Reproductive investment

The physical nest-site features that I assessed did not influence clutch initiation dates in 2008; however, between 1990 and 1997, initiation was earlier in boxes associated with higher small mammal indices. This relationship was more strongly predicted by voles, but higher numbers of other small mammals also significantly advanced laying. Where food is more abundant near nest sites, females (via males) have the potential to increase their rates of food consumption and become ready to produce eggs earlier. The rate of food intake per day is known to be negatively correlated with the onset of laying and experiments with kestrels and other raptor species have shown laying to advance in response to food supplementation (Meijer et al. 1989). My result provides further evidence for the proximate role of food in determining the timing of breeding.

Although vole indices were the more important influence on clutch initiation date, they did not significantly influence clutch size between 1990 and 1997. However, on territories where the number of all other small mammals was greater, clutch sizes were slightly larger, although this result only approached significance. From 1990-1992, Wiebe and Bortolotti (1995) found that egg size among 5-egg clutches was positively correlated with the abundance of all small mammals on each territory in May in my location. My marginal positive effect of small mammals on clutch size may be a function of the fact that I was able to evaluate clutch size over an eight year period allowing for detection of subtle variability. Red-backed voles are the main prey source of kestrels in this location, and yet vole indices did not predict clutch size. In all years except 1992, the other small mammal index in May was higher than, or similar to, vole indices; however, in all years, the vole index in July was higher than other mammals (Fig. 3). Adults should time clutch initiation so that the peak energy requirements of nestlings correspond with peak availability of major food sources (Thomas et al. 2001) and egg production is known to be influenced by food abundance via parental condition (reviewed in Martin 1985, Wiebe and Bortolotti 1995). Here, it appears that adults synchronized the timing of clutch initiation so that brood-rearing coincided with the prey source that was most abundant during that time; however, clutch size was proximately influenced by the prey source most abundant at the time of clutch initiation, when this energy is directly mobilized to egg production.

I did measure eggs in 2008 to obtain clutch volume and found that females in deciduous disturbed habitats invested significantly less in eggs than in all other surrounding composition types, including the burn, except for recently harvested. Given that kestrels in my study location have been shown to adjust egg size in response to food, this difference in clutch volume among surrounding composition types could be the result of variable prey availability among different forest types prior to and during laying.

2.5.3 Reproductive success

Boxes located in the burn fledged, on average, 0.88 (± 0.49) more young than all other boxes, although this result was not statistically significant ($P = 0.08$). These boxes possessed no vegetative cover, regardless of orientation, which may have resulted in more favourable (warmer) thermal regimes due to exposure to direct sunlight. Although I lack data to specifically test this idea, warmer temperatures in natural and artificial cavities have been shown to increase clutch size (Wiebe 2001) and nestling growth and survival (Dawson et al. 2005) of other cavity nesting birds. The fact that males were in better body condition in the burn than in all other areas indirectly suggests that the nestlings of these males were likely to receive higher quality of parental care from both the males and the higher quality females which mate with them (Bortolotti and Iko 1992). The pine regeneration in the burn is of a height that maintains an open overhead canopy interspersed with residual snags, which are used for perching. This landscape composition may be well-suited to predators that hunt visually from above and allow kestrels to hunt further from the nest without sacrificing the ability to detect and mitigate threats to the nest. For nestlings, these factors would ultimately result in increased energy acquisition, and lower risk of predation.

Female nestlings were affected by two nest-site scale characteristics, distance to edge and tree species. At day 24, female nestlings in boxes located at forest's edge were over 8 g heavier than those away from edge, and females in boxes located on jack pine trees were over 10 g heavier than those on aspen trees. In addition, I found that the tenth primaries of males were longer in boxes mounted on unhealthy and dead trees than on live trees, although this difference was significant only for the unhealthy category. I hypothesize that these mass or feather length advantages are a function of increased accessibility to prey allowing for greater parental provisioning. Nests located at the edge or in recently harvested areas may be more readily accessible to parents during provisioning and allow adults a clear line of sight to maintain vigilance while hunting which would maximize the amount of time available for provisioning. Nest trees that contain some dead branches also provide a clearer line of sight and near-by perches, both of which would benefit hunting effort. Furthermore, mature stands are the most suitable for red-backed voles (Fischer and Wilkinson 2005) and jack pine that are large enough to house nest boxes are a dominant component of mature stands in my study area. American kestrels exhibit sexual size dimorphism so it is not surprising that I would find nest site features to influence female mass but male feather length. Female nestlings do not show competitive dominance for food when nestlings are fed small mammals, as they can with smaller food sources (e.g. insects; Anderson et al. 1993). Assuming adequate availability of small mammals and equal access to food, male nestlings can invest residual energy in feather growth once they achieve asymptotic mass. Female nestlings must achieve greater mass, so if a nest realizes a food advantage, then female nestlings may invest the additional resources into structural and dynamic tissue growth before fledging.

The location of the nest box on the tree (height, orientation etc.) had no influence on settlement or reproduction; rather, most of the associations that I found appear to be indicators of ecological interactions and factors influencing parental behaviour. It is evident that breeding site features measured across all scales influence settlement and reproduction and I predicted that these associations may be a function of variable predation risk, and prey abundance and accessibility. Further research will be required to determine links between habitat features at the nest and territory scale, and interspecific interactions, parental behaviour, and breeding outcomes. Such studies should clarify the relative importance of the factors associated with these scale-specific habitats that affect decision making, and the proximate causes for the differences in reproductive success that I observed. I was surprised to find that prey abundance was not a reliable predictor of nest-site selection; however given the results of others (i.e. Smallwood et al. 2009b) concerning the importance of patch size in nest box occupancy, I would argue that habitat suitability, including prey abundance, should be measured against nest-site selection at a larger scale.

3. Risk of nest predation influences reproductive investment in American kestrels (*Falco sparverius*): an experimental test.

3.1 Abstract

Nest predation is the primary cause of nest failure in birds. Individuals should therefore adjust parental investment to minimize the costs associated with this constraint; evidence suggests that nest predation influences nest-site selection, and drives variation in both clutch size and parental behaviour. Here, I test how the perception of the risk of nest predation from red squirrels (*Tamiasciurus hudsonicus*) influenced nest-site selection and reproductive investment of American kestrels (*Falco sparverius*) breeding in the boreal forest. For this purpose, I conducted audio playbacks of squirrel vocalizations and altered nest boxes to experimentally increase cues of the presence of Red squirrels in the vicinity of potential nests. Experimental manipulations of the risk of nest predation did not influence nest-site selection; however, experimentally increasing the perceived risk of nest predation induced kestrels to initiate breeding later, and to lay larger clutches. Parents did not appreciably alter incubation behaviour in response to my manipulation, although the duration of incubation was longer where natural squirrel threat was higher. My results showed that kestrels are capable of making facultative adjustments to current reproductive investment in response to their perception of the risk of nest predation.

3.2 Introduction

Although resource availability is thought to drive variation in life-history strategies (Martin 2002), nest predation is the primary cause of nest failure in birds (Ricklefs 1969, Martin 1995) and a key predictor of productivity (Thompson 2007). During breeding, birds may incur costs associated with resource limitation, competition, sub-optimal weather, and predation risk (Martin 1996, Fontaine and Martin 2006a); minimizing these costs should contribute to overall fitness (Martin 1998, Smith et al. 2000, Morris 2003). The risk of nest predation, defined as risk of mortality or danger (the probability of mortality) imposed by a predator (Lank and Ydenberg 2003), should therefore be an important constraint driving the evolution of avian parental investment strategies. For example, risk of nest predation has been shown to influence nest-site selection and induce breeding dispersal in a number of avian species, and in some systems nest predation affects variation in clutch size and parental behaviour (reviewed in Lima 2009).

Decisions concerning space-use are understood to be influenced chiefly by the distribution and abundance of both resources and predators (Willems and Hill 2009). If habitat selection is adaptive, it should confer increased reproductive success (Martin 1998), so when all else is equal, birds should choose a nest site with the lowest possible risk of nest predation. To assess the risk of nest predation, settling individuals may use past experience; most studies to date have examined the influence of nest predation on nest-site selection in subsequent years (e.g., Doligez and Clobert 2003). Individuals may also use indirect cues from conspecifics or heterospecifics, but direct cues are presumably the most reliable (Thomson et al. 2006). Researchers assessing parental decision-making typically describe the trade-offs animals make among both direct and indirect influences on breeding-site selection (Brown 1988) but have seldom measured the perception of predation risk as opposed to actual predation risk (but see Fisher and Wiebe 2006).

Theory predicts that increased nest predation will select for reduced clutch size (Lima 1987, Martin 1993), which allows for shorter laying and nestling periods, smaller and less conspicuous nests, more satiated (quieter) young, and fewer parental nest visits during the nestling phase. These allowances provide parent birds the advantage of fewer opportunities for nest detection by predators, and a reduction in both the period of time eggs and nestlings are exposed to predators and the amount of time parents must engage in anti-predator behaviour (Skutch 1949, Martin et al. 2000a, 2000b). Furthermore, smaller clutches require less energy, thereby increasing an adult's chance of successfully producing and rearing a second brood should the first be depredated (Martin 1995). Although lower rates of nest predation are thought to account for larger clutch sizes in cavity nesting birds (Martin and Li 1992), there is limited support for this and the effect of nest predation on reproductive strategies of cavity nesters remains equivocal.

Although there is evidence that nest predation is a factor in shaping the evolution of clutch size, the influence of nest predation on other aspects of reproductive investment is less studied. There is little evidence for the role of parental evaluation of the risk of nest predation in influencing initiation date and if, as Skutch (1949) hypothesized, greater parental activity at the nest increases nest predation, then birds should adjust their incubation behaviour to minimize the amount of attention they draw to the nest. The behaviour of incubating parents directly influences hatching success (Ghalambor and

Martin 2002) but few (e.g., Fontaine and Martin 2006b) have experimentally tested how parents may adjust incubation rhythms in response to nest predation.

I tested the hypothesis that the perception of the risk of nest predation drives variation in nest-site selection and reproductive investment of American kestrels (*Falco sparverius*) in the boreal forest of north-central Saskatchewan, Canada. American kestrels (hereafter, kestrels) are secondary cavity nesters and in my study area, red squirrels (*Tamiasciurus hudsonicus*) prey on kestrel eggs and hatchlings, and are also an important nest competitor (Dawson and Bortolotti 2006a). The causes and consequences of settlement decisions of this species are poorly understood; little is known about how kestrels perceive predation risk, and whether their perceptions influence their anti-predator decision making. I conducted audio playbacks of squirrel vocalizations and altered nest boxes to experimentally increase cues of the presence of red squirrels in the vicinity of potential nests. I predicted kestrels would use these cues to preferentially select nest sites associated with lower perceived risk of predation, and adjust reproductive investment and incubation behaviour to minimize the anticipated costs associated with higher predation risk.

3.3 Methods

3.3.1 Study area

I studied American kestrels breeding in nest boxes in the boreal forest near Besnard Lake, Saskatchewan (55° N, 106° W). The study area comprised a network of nest boxes situated along gravel roads. Nest boxes were located either in mature mixed forests composed of both deciduous and coniferous cover or adjacent to harvested cut blocks with regeneration (jack pine, *Pinus banksiana*) lower than the height of the box. Kestrels begin arriving on the study site in mid- to late April (Dawson and Bortolotti 2002); my experiment was conducted between late April and July, 2008.

3.3.2 Cues of predation risk

I used playbacks of red squirrel vocalizations as cues to simulate the presence of a territorial squirrel near nest boxes. Although visual cues may signal the potential risk of nest predators, I chose squirrel vocalizations because these would seem a direct representation of reality in comparison with other approaches such as a dummy display. In addition, kestrels are sensitive to researcher presence near the nest box during the initiation phase, and the use of a playback allowed me to minimize the time I spent near the nest box while maximizing exposure to the cue. I chose nest boxes that kestrels had bred in at least once during the previous five years; 29 of these were randomly assigned as experimental boxes, 29 were assigned to the control group. I created playback recordings that were a combination of warning barks, chips, and trills of red squirrels interspersed with silence. These were broadcast at experimental boxes on a continuous loop for 7-12 hr, every third day, beginning 28 April. Squirrel vocalizations were played from a small compact disc player (Durabrand, model CD-566, Lennox Electronics Corp., Edison, New Jersey, U.S.A) with portable speakers (ILO Digital Active Speaker System, DSP-26A, 1.5 W RMS, Lennox Electronics Corp., Edison, New Jersey, U.S.A); the playbacks were audible to me at a distance of at least 100 m. Male kestrels establish territories; however, upon pair formation, females may choose from multiple nest holes that the male presents to her (Balgooyen 1976; J. Greenwood *unpubl. data*); thus, in order to concentrate the audio cues around only my nest boxes, I placed speakers 20 paces from the nest box in a random direction. Kestrels feed on a diverse array of prey, including birds (Dawson and Bortolotti 2006a); therefore, I did not subject control boxes to playbacks of a non-predator (e.g., songbird) to avoid confounding effects of perceived resource availability or distribution. Rather, I visited a random location, 20 m from each control box, on the same schedule as experimental boxes. Playbacks were conducted until laying was largely finished throughout the study area and, in the case of occupied boxes, until hatching.

In addition to audio playbacks, I altered nest boxes slightly to simulate use or prospecting by red squirrels. In the early stages of nest-building, squirrels often deposit neatly wound balls of grass in nest boxes before constructing a full nest of grass and leaves. Furthermore, boxes frequented by squirrels routinely exhibit chewed entrance holes. I mimicked these two cues to simulate the presence of squirrels on the territory and in the box. I placed three balls of grass (collected from squirrel nests throughout the study area) in each experimental box, and the entrance holes of the boxes were chiseled (but not enlarged) in a manner similar to the incisor marks left from squirrels. Control boxes were left empty, and entrance holes were not altered.

3.3.3 Nest-box selection and reproductive rate

Starting in early May, I visited nest boxes every 3-5 days to determine selection of boxes as nest sites, and clutch initiation dates in those boxes where eggs were laid. Upon clutch completion, I returned to determine clutch size and measure eggs; at this time I also captured adults by hand in nest boxes. I measured the length (l) and breadth (b) of each egg, and for male and female parents I measured length of tarsus, culmen, 10th primary feather, central and outer rectrices, and unflattened wing chord. I also recorded mass, and scored the integumentary color of the cere, lores, and tarsi on a six-point scale (Dawson and Bortolotti 2006b); on my scale, a lower score indicates brighter coloration.

Although the first individuals to arrive on a breeding area are thought to secure the highest quality nest sites (Fontaine and Martin 2006a), intraspecific interactions as a result of mate choice and resource limitation (food, nest sites) may complicate this relationship. The outcome of these interactions can be a function of individual quality, and so I examined several measures to test whether the quality of males and females differed among those that chose control or treatment boxes. I calculated two measures of adult quality. First, I used the first component (PC1) of a principle components analysis (PCA) that was calculated using the six linear size measurements taken from all adults (first capture only) caught on the study area in 2007 and 2008. Data from males (n = 130, 49.89% variance explained) and females (n = 105, 48.30% variance explained) were analyzed separately (Bortolotti and Iko 1992). As an index of body condition of male parents I used the residuals from a linear regression of body mass, measured during incubation, on PC1 (Dawson and Bortolotti 2000). Body condition of kestrels can vary during the breeding season (Dawson and Bortolotti 1997); however, I detected no relationship between capture date and condition residuals so did not correct for capture date. There was no relationship between mass (measured during incubation) and PC1 (r = 0.01, P = 0.90, n = 99) among females in my study area in 2008, so I used mass as a proxy.

The second measure of adult quality I used was the sum of color scores for the cere, lores, and tarsi. Skin color is correlated with carotenoid concentration in plasma (Bortolotti et al. 2003), and is influenced by prey abundance (Bortolotti et al. 1996), and indirectly, an individual's ability to secure prey. In addition, carotenoid-dependent color may signal the ability to manage parasite infections (Dawson and Bortolotti 2006b), and although environment-dependent, skin color is regulated in a manner that suggests it is a sexually selected trait (Negro et al. 1998). Consequently, in addition to body condition, integumentary color may be considered one measure of individual quality (Bortolotti et al. 1996).

3.3.4 Incubation behaviour

During visits to nests to capture adults, a data logger was installed in some nests to monitor incubation patterns. A small probe was fitted with a rubber sleeve (to prevent damage to the eggs), threaded through the bottom of the nest box, and secured in a position in the middle of, and flush with, the top of the eggs. Probes were connected to HOBO data loggers (Onset Computer Corporation, Massachusetts, U.S.A) which were programmed to record the temperature at the tip of the probe every 1.6 min.

I used the program Raven and the plug-in Rhythm (Cooper and Mills 2005) to determine the periods when an adult was incubating the eggs (on-bouts) and periods of non-attendance (off-bouts), based on temperature fluctuations. I validated my interpretations by verifying that off-bouts were recorded at the times I captured an adult from the nest (n = 7). Off-bouts were not verifiable or readily interpretable for all nest boxes, and some nests were abandoned some time after I installed the probes, so sample sizes for these analyses varied. To maximize sample size, I analyzed incubation rhythms of each box for only one 12-hr period. This 12-hr period was between 08:00 and 20:00 H, within 3 d following installation of the temperature loggers, and on a treatment (playback or control) day, between 9-16 d after clutch completion. I chose a day soon after installation in the event that adults in treatment boxes became desensitized to the playbacks.

3.3.5 Quantifying natural squirrel threat

I estimated the density of red squirrels by conducting surveys in the vicinity of each nest box, over a period of 3 d, within the first week of beginning playbacks. Three parallel transects were walked, within 100 m of each box; the middle transect began in a randomly determined direction 25 m from the box. Each line was 50 m long, and 50 m from adjacent grid lines. When feeding, squirrels leave behind piles of cone-bracts which can become large over time. In addition, they often leave obvious signs of digging when burying or searching for food (fungi, cones) in the moss layer (Mahon and Martin 2006). I tallied the total number of feeding piles and digging sites encountered within a 4-m swath of grid lines at each nest site (3 transects). I also tallied the number of squirrels encountered (seen or heard) within a 100-m belt of grid lines, taking care to count each individual only once (Mahon and Martin 2006). I conducted these transects near the beginning of the experiment to determine squirrel density at a time when most birds are arriving and prospecting. I also recorded whether squirrels were detected (seen or heard within 100 m of nest boxes) at each nest visit (two per day, every third day) and calculated the proportion of visits on which squirrels were detected for each nest site.

To control for squirrel density and prevalence I calculated an index of natural squirrel threat using PC1 (52.76% variation explained) from a PCA that included for each nest site the total number of feed piles, total number of digs, number of squirrels detected (seen or heard), and the proportion of visits where a squirrel was detected (seen or heard). Higher (more positive) values of PC1 are associated with greater numbers of feed piles, digs, and squirrel detections at each site.

3.3.6 Data analysis

I used binary logistic regression to asses nest-site (box) selection (selected, unselected) as a function of experimental manipulations (control, treatment), surrounding habitat composition (mature mixed forest, harvested), natural squirrel threat (PC1), and treatment-by-squirrel threat interaction. I used a backwards stepwise approach to sequentially remove terms that did not improve model fit. I evaluated each model by comparing the log-likelihood to that of the null model using a goodness of fit χ^2 to test the null hypothesis that at least one of the coefficients equalled zero (Quinn and Keough 2002). The inclusion of predictor terms was evaluated by using the likelihood ratio test to determine loss of fit with the individual exclusion of each variable in a given model; I used this in addition to the Wald statistic because it yields greater power with small sample sizes (Quinn and Keough 2002).

I used analysis of covariance (ANCOVA), with natural squirrel threat as a covariate, to test whether male or female body condition or integumentary color differed among individuals that chose treatment or control nests. I also tested for differences in the size of males and females according to treatment; size can influence the energy budget

(Vedder et al. 2005) and aerial agility (Bortolotti and Iko 1992) of kestrels and therefore may influence the ability to secure a mate, and provision nestlings.

I used ANCOVA to test for the effects of treatment on clutch-initiation date, clutch size, mean egg volume in each nest, hatching success, percent of time spent off the nest during incubation, mean incubation off-bout duration, number of incubation off-bouts per 12 hr, and duration of incubation. Treatment group was the categorical variable and natural squirrel threat was the covariate in each model. Although kestrels usually begin continuous incubation when the third egg is laid (Bortolotti and Wiebe 1993), I could not confirm that all birds began incubating at this time, so I calculated a coarse estimate of the duration of incubation as the number of days between clutch completion and the day the first egg hatched. Egg volume was calculated as $0.51*l*b^2$ (Hoyt 1979) and hatching success was calculated as the ratio of the number of nestlings hatched to the number of eggs laid. For analyses of clutch size and egg volume, I also included mass of females and clutch initiation date as additional covariates, and for analyses of hatching success, clutch size and male size were included as additional covariates. For all analyses I iteratively removed terms that did not approach significance ($P < 0.10$), but I included experimental treatment as a fixed factor and natural squirrel threat as a covariate in all final models because I was interested in both the influence of my experiment and the background risk of nest predation from squirrels on the variables I tested.

All data were examined visually and statistically for distributional violations. Parametric tests were used in all cases because I detected no severe departures from normality, and no statistically significant inequality of group variance. In cases where the homogeneity of regression slopes assumption was violated, I examined each experimental group individually. All analyses were performed using SPSS 13.0 (Norušis 2000) and results were considered significant at $P = 0.05$. I present means ± 1 SE and show final statistical models only.

3.4 Results

A summary of mean reproductive measures collected in 2007 and 2008 are provided in Table 3.1. Statistics for 2007 are included as a reference for a year in which this experiment was not conducted.

3.4.1 Nest-box selection

Kestrels initiated clutches in seven treatment, and nine control boxes ($n = 29$ boxes for each experimental group). The logistic regression model including treatment group and squirrel threat as explanatory variables performed significantly better than the null model ($\chi^2_2 = 6.42$, $P = 0.04$). In this model, neither treatment group ($\beta = 0.61, \pm 0.60$ SE, Wald = 1.01, $P = 0.32$) nor natural squirrel threat ($\beta = -0.99 \pm 0.54$ SE, Wald = 3.42, $P = 0.06$) had coefficients that were significantly different from zero; however, natural squirrel threat approached significance, and the fit of the full model was significantly better than the reduced model that excluded natural squirrel threat ($\chi^2_1 = 3.79$, $P = 0.05$), but not treatment group ($\chi^2_1 = 1.29$, $P = 0.26$). This indicates that although my manipulations of perceived predation risk did not affect nest-site selection, the threat imposed from background squirrel presence near potential nest sites likely had some negative influence on nest-site selection (Fig. 3.1).

Table 3.1. Summary statistics of reproductive measures of American Kestrels (*Falco sparverius*) breeding in north-central Saskatchewan in 2007 and 2008. Statistics for 2007 are provided for reference

		Julian Clutch-Initiation Date			Clutch Size			Hatching Success			Number of Young Fledged		
Year	Experimental Group	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
2007	None	134.70	1.16	115-173	4.94	0.09	2-7	0.64	0.06	0-1	2.81	0.30	0-5
2008	None	142.51	1.18	128-162	4.60	0.09	3-5	0.83	0.06	0-1	3.20	0.25	0-5
	Control	137.38	1.48	134-145	4.75	0.16	4-5	0.72	0.16	0-1	2.38	0.75	0-5
	Playback	145.86	2.28	136-153	4.57	0.37	3-6	0.40	0.19	0-1	0.71	0.71	0-5

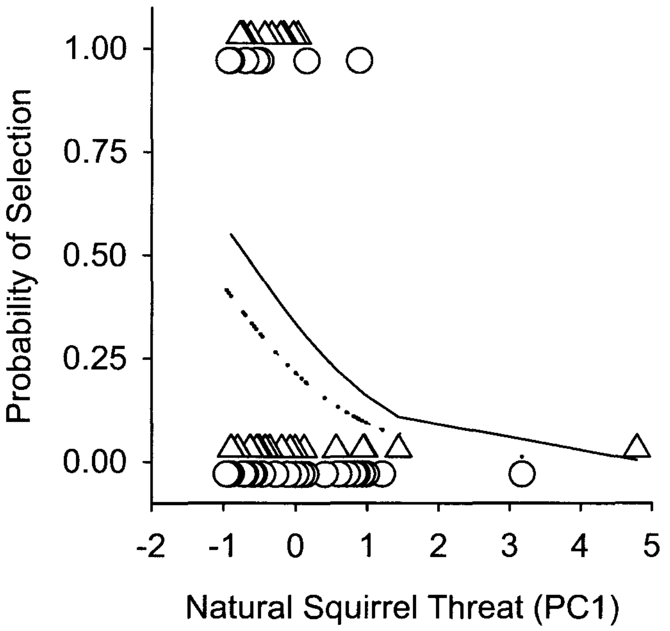

Figure 3.1 Observed and predicted probabilities of American Kestrels (*Falco sparverius*) selecting nest boxes where the perceived risk of nest predation was experimentally increased (open circles, dashed line) or control boxes (open triangles; solid line) in relation to the natural threat of nest predation imposed by squirrels present in the vicinity of nest boxes. Observed values have been slightly offset by treatment group to illustrate their distribution on the plot.

There were no differences in male or female size (PC1), male condition, female mass, or male color scores between individuals that selected treatment versus control nests; natural squirrel threat was not significant in any of these analyses (Table 3.2). Although the integumentary color of females that nested in treatment boxes was duller than those in controls, there was a significant interaction between treatment and natural squirrel threat so I was unable to test the significance of this difference using an ANCOVA. Analyses conducted separately for each treatment group showed that in control boxes, females with duller (higher) color scores during incubation settled in boxes with a higher natural squirrel threat ($r = 0.77$, $P = 0.01$, $n = 9$), whereas in treatment boxes, I detected no relationship ($r = 0.01$, $P = 0.99$, $n = 6$).

3.4.2 Reproductive effort

Although natural squirrel threat affected nest-site selection, it did not significantly influence clutch-initiation date, clutch size, mean egg volume, or hatching success (Table 3.3). Kestrels that laid clutches in treatment boxes initiated later than kestrels that laid clutches in control boxes (Fig. 3.2a, Table 3.3). After controlling for clutch-initiation date, I found that clutch sizes in the treatment group were larger than those in the control group (Fig. 3.2b, Table 3.3). I found no difference between experimental groups in mean egg volume or hatching success, although hatching success was positively related to clutch size and negatively related to male size (Table 3.3). I observed that more pairs that nested in treatment boxes appeared to abandon their nests altogether prior to hatching (4 out of 7) than those that nested in control boxes (2 out of 9); however, a logistic regression showed that neither playback treatment nor natural squirrel threat predicted

Table 3.2. ANCOVA parameters of final models testing for differences in individual adult quality among American Kestrels (*Falco sparverius*) that chose nest boxes where perceived threat of predation was experimentally increased or control nest boxes. Natural squirrel threat is an index of the background risk of nest predation posed by squirrels using PC1 from a PCA that included four measures of squirrel presence at each nest site

	MEAN ± SE^a					
DEPENDENT VARIABLE	CONTROL	PLAYBACK TREATMENT	INDEPENDENT VARIABLES^b	*F*	df	*P*
Female size (PC1)	0.52 ± 0.46	-0.46 ± 0.46	Experimental group	2.30	1,11	0.16
			Natural squirrel threat	0.71		0.42
Female mass (g)	132.67 ± 4.37	128.67 ± 4.33	Experimental group	0.35	1,12	0.56
			Natural squirrel threat	0		0.99
Female color	10.67 ± 0.62	11.17 ± 0.54	Experimental group	2.08	1,11	0.18
			Natural squirrel threat	7.14		0.02
			Experimental group-by-natural squirrel threat	7.23		0.02
Male size (PC1)	-0.10 ± 0.34	-1.13 ± 0.57	Experimental group	3.53	1,10	0.09
			Natural squirrel threat	0.01		0.94
Male condition	-3.44 ± 2.32	-0.41 ± 1.73	Experimental group	0.78	1,10	0.40
			Natural squirrel threat	0.01		0.93
Male color	7.63 ± 0.42	7.0 ± 0.32	Experimental group	1.09	1,10	0.32
			Natural squirrel threat	1.31		0.28

[a] Raw means

[b] In all cases, experimental group is the independent variable of interest, subsequent independent variables are covariates.

Table 3.3. ANCOVA parameters for final models testing for differences in reproductive effort and incubation vigilance of American Kestrels (*Falco sparverius*) that chose nest boxes where perceived threat of predation was experimentally increased or control nest boxes. Natural squirrel threat is an index of the background risk of nest predation posed by squirrels

	MEAN ± SE[a]					
DEPENDENT VARIABLE	CONTROL	PLAYBACK TREATMENT	INDEPENDENT VARIABLES[b]	*F*	df	*P*
Julian clutch-initiation date	138.27 ± 1.73	145.94 ± 1.96	Experimental group	8.60	1,13	0.01
			Natural squirrel threat	2.10		0.17
Clutch size	4.25 ± 0.21	5.14 ± 0.23	Experimental group	6.52	1,11	0.03
			Natural squirrel threat	1.10		0.32
			Clutch initiation date	19.34		0.001
Mean egg volume (cm^3)	14.23 ± 0.33	14.44 ± 0.41	Experimental group	0.16	1,11	0.70
			Natural squirrel threat	0.003		0.96
			Female mass	5.41		0.04
Hatching success	0.47 ± 0.15	0.50 ± 0.18	Experimental group	0.01	1,10	0.93
			Natural squirrel threat	1.07		0.34
			Clutch size	5.57		0.05
			Male size (PC1)	4.65		0.07
Time off (%)	7.10 ± 2.10	7.40 ± 2.70	Experimental group	0.01	1,7	0.95
			Natural squirrel threat	0		1
			Clutch size	4.26		0.085
Number of off-bouts/12 hr	7.04 ± 1.65	5.17 ± 2.25	Experimental group	0.41	1,8	0.54
			Natural squirrel threat	0.26		0.62
Incubation duration (d)	26.76 ± 0.44	28.48 ± 0.62	Experimental group	5.08	1,6	0.065
			Natural squirrel threat	6.19		0.047

[a] Marginal means, [b] In all cases, experimental group is the independent variable of interest, subsequent independent variables are covariates

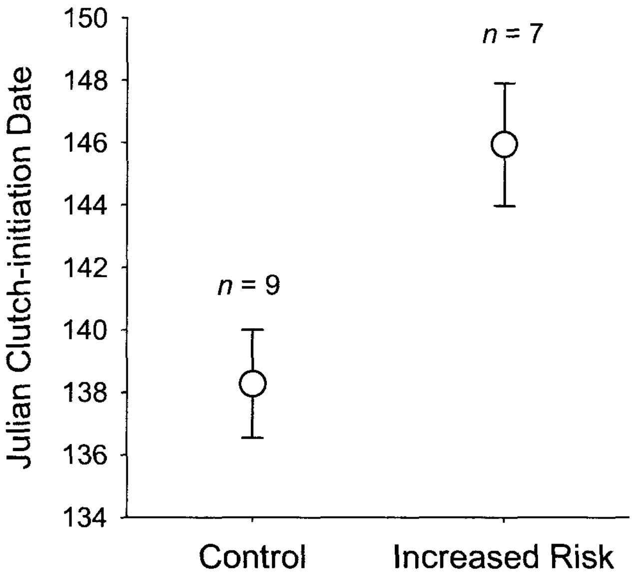

Figure 3.2a Marginal means (± 1SE) of Julian clutch-initiation dates of American kestrels (*Falco sparverius*) that initiated breeding in control nest boxes and boxes where the perceived risk of nest predation was experimentally increased, after controlling for natural squirrel threat.

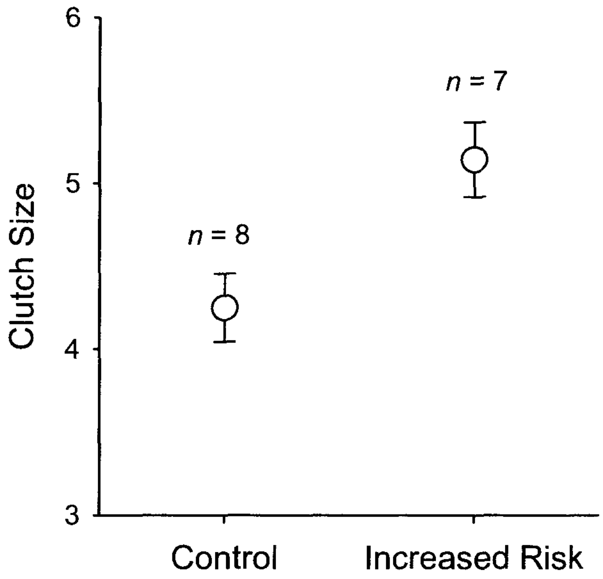

Figure 3.2b Marginal means (± 1SE) of American kestrels (*Falco sparverius*) that initiated breeding in control nest boxes and boxes where the perceived risk of nest predation was experimentally increased, after controlling for clutch-initiation date and natural squirrel threat.

abandonment ($\chi^2_2 = 2.37$, $P = 0.31$).

3.4.3 Incubation behaviour

There was a non-significant trend for percent of time nests were left unattended to decrease with larger clutches, but I found no experimental effect on the percent of time off nests, or on the number of off-bouts in a 12-hr period (Table 3.3). Although mean off-bout duration was slightly longer for playback treatment nests (9.68 min ± 1.95) than controls (9.12 min ± 1.75), the assumption of homogeneity of regression slopes was violated (natural squirrel threat-by-experimental group: $F_{1,12} = 6.33$, $P = 0.04$; Fig. 3.3) so I did not examine this difference for statistical significance. Both experimental and control groups showed positive relationships between natural squirrel threat and off-bout duration, but this was significant only for the control nests (Fig. 3.3). In addition, hatching success decreased as the mean off-bout duration increased ($r = 0.70$, $P = 0.02$, $n = 11$).

Natural squirrel threat was a significant covariate in my analysis of incubation duration, and although mean incubation duration was longer for treatment boxes, this effect only approached significance (Table 3.3). It is also noteworthy that although sample sizes were limited, correlation analyses showed that boxes with longer mean off-bout durations had longer incubation durations ($r = 0.80$, $P = 0.02$, $n = 8$).

3.5 Discussion

3.5.1 Nest-box selection

I directly manipulated cues of the risk of nest predation to determine the

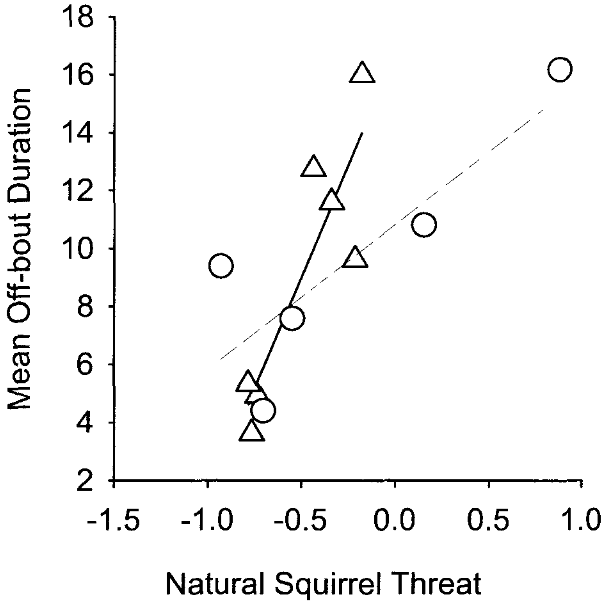

Figure 3.3 Mean off-bout duration (min) of American Kestrels (*Falco sparverius*) in control boxes (open triangles, solid line; $r^2 = 0.78$, $P = 0.008$) and boxes where the perceived risk of nest predation was experimentally increased (open circles, dashed line; $r^2 = 0.73$, $P = 0.065$) in relation to natural squirrel threat.

importance of this interspecific interaction on nest-site decisions. Increasing the perceived risk of nest predation by using squirrel vocalizations and altered nest boxes did not have a direct influence on nest-site selection by American kestrels in my study area. Males establish territories, and for females, the choice of a mate likely involves not only an assessment of the individual male, but of the quality of the territory he has secured. Ultimately, females choose a nest site from among several the male may present to her on his territory (Balgooyen 1976); this is the finest scale decision made with regard to breeding habitat selection (Orians and Wittenberger 1991). This series of decisions should factor in the relative value of potential nest sites so that, on balance, the chosen nest site is one that will maximize fitness (Martin 1998, Morris 2003, Fontaine and Martin 2006a). I controlled for background levels of the threat of nest predation, and examined settlement outcomes with respect to individual quality, but I did not quantify all possible factors that may signal nest-site quality and interact with the risk of nest predation to influence parental decisions. For example, resource availability (e.g., food availability, the number of potential nest sites/territory) is known to influence reproductive success of kestrels (Wiebe and Bortolotti 1994, Dawson and Bortolotti 2000, 2002) and may also have played a role in nest-site selection.

Although I made small physical adjustments to experimental nest boxes to mimic use by squirrels, the primary cue that I used was auditory. My results showed that these cues did not significantly alter nest selection behaviour, but that the natural squirrel threat did. All but one of the measures of natural squirrel threat that I used were visual cues. If a squirrel is detected near a box, either by sight or sound, it may be a resident of that territory, or simply moving through the area. Consequently, an audio cue may not be the most reliable indicator of the threat of squirrel presence throughout the nesting phase, whereas physical (visual) cues such as digging and feeding piles, which can grow large over time, are indicative of the persistent presence of squirrels in an area. Kestrels may utilize these physical cues as indicators of the long-term threat imposed by squirrels when assessing potential nest sites. Furthermore, kestrels hunt by sight and may also rely most heavily on visual cues in their initial assessment of predation risk.

I found no indication that adults that had brighter integument color or were in better condition were more likely to nest in control boxes (Table 3.2). However, skin color and condition can vary throughout the different phases of breeding (Dawson and Bortolotti 1997, 2006b) so it is possible that I found no pattern in settlement as a function of adult quality because I captured and measured adults during incubation rather than settlement. Among females that nested in control boxes, those that were duller during incubation nested in boxes with higher natural squirrel threat, but differences in color, mass, or size of females that nested in treatment boxes did not differ from those in control boxes. So although I found a relationship between female color and natural squirrel threat in control boxes, my results are not suggestive of the idea that higher quality adults were more successful at securing boxes they perceived to be associated with a lower risk of nest predation. Alternately, there was little suggestion that there may be some cost to nesting in boxes with a higher perceived risk of nest predation.

3.5.2 Reproductive investment

Birds that initiate breeding earlier typically realize higher reproductive success; this may occur as a function of parental quality or temporal changes in the environment that influence resource availability, resulting in lower survival probability of avian offspring with later onset of breeding (Verhulst and Nilsson 2008). I found that birds that chose treatment nests initiated breeding more than one week later than pairs that selected control nests. If this were a function of competitive interactions that resulted in lower quality birds selecting treatment boxes, I would have expected to detect differences in adult quality between those that settled in treatment and control boxes. Given that I found no evidence of such differences, I suggest a facultative delay in the timing of breeding by kestrels. It is possible that once females selected a mate whose territory included a treatment box, they required a longer period of time to weigh the benefits of breeding in treatment boxes against the associated risk of nest predation that they perceived. Alternatively, treatment boxes may have been occupied by later-arriving pairs. Still, the occupation of these boxes would indicate the benefits were perceived to outweigh the risks because not all control boxes were occupied and so were also available for use.

The increase in clutch size that I observed is contrary to both theory and empirical evidence suggesting that birds reduce clutch size in response to increased nest predation (Slagsvold 1984, Doligez and Clobert 2003, Eggers et al. 2006). Martin and Li (1992) found that secondary cavity nesters (non-excavators) had larger clutch sizes than primary cavity nesters (excavators) or open cup nesters, even though they experienced higher failure rates than excavators. Subsequently, Martin (1993) suggested that the evolution of clutch size in cavity nesting birds is driven by variation in nest-site limitation more than nest predation; non-excavators are more constrained by the availability of nest sites than excavators. Although squirrels can depredate entire clutches or young broods, often only partial clutch loss occurs (J. Greenwood *unpubl. data*). Double-brooding has not been documented at my study area, so where nest sites and subsequent breeding attempts are limited, a facultative increase in clutch size may increase a pair's chance of fledging at least one young during their first attempt, even if they experience partial predation of their clutch.

It is also possible that the increase in clutch size I observed was a function of the delay in clutch initiation. This delay allowed females in treatment boxes an additional week to acquire nutrients, which may have enabled them to lay more eggs. Studies of Eurasian Kestrels (*F. tinnunculus*) have shown that the typically negative relationship between clutch-initiation date and clutch size can become decoupled when food availability is manipulated (Aparicio 1994). Regardless, previous experiments conducted at my study area indicated that although kestrels laid larger eggs in response to food supplementation, they did not increase clutch size (Wiebe and Bortolotti 1994). I did not observe any difference in mean egg volume of birds that initiated breeding later (Table 3.3), and so it seems unlikely that acquisition of additional nutrient reserves by delayed females can account for my results.

Red squirrels have been observed using parental activity to locate nests of open cup and cavity nesting passerines (Ghalambor and Martin 2002), and heightened parental activity at the nest is associated with significant proximate increases in nest predation in open-cup and ground-nesting birds (Wiebe and Martin 1997, Martin et al. 2000b). Faced with increased nest predation, open-cup nesters have been shown to adopt longer on- and off-bout durations thereby reducing activity at the nest (Conway and Martin 2000). I found that off-bout durations were indeed longer at nest sites with higher natural squirrel threat, but was unable to evaluate the significance of longer off-bout durations in playback treatment nests.

Although the effect of experimentally increased risk of predation on off-bout duration was inconclusive, the incubation duration was 1.7 d longer than that in control boxes. This delay approached significance, and higher natural squirrel threat also produced longer incubation periods (Table 3.3). Short incubation periods have been shown to increase hatching success in other birds (e.g. Lyon and Montgomerie 1985) and my data showed that hatching success decreased with longer mean incubation duration. This relationship suggests an indirect cost to the perception of increased risk of nest predation. However, although parental decisions that result in decreased hatching success lead to reduced fitness (Brown 1988), the cost is presumably lower than would be incurred in the event of complete nest failure in the absence of anti-predator strategies.

My manipulations showed that kestrels adjust their reproductive strategies in response to the risk of nest predation they perceive, but further studies are required to establish the cause of delayed clutch initiation, and the ultimate function of, and mechanism for, increased clutch sizes. The increase in clutch size that I observed in experimental boxes would be of enhanced interest if, in fact, lower quality females were securing higher risk boxes and initiating later. In this case, I would expect reduced clutch sizes in these nests. Larger, longer-term studies may clarify this phenomenon, in addition to whether and how kestrels adjust incubation behaviour in response to this constraint. Theory surrounding the role of nest predation in influencing reproductive decisions will be greatly improved by an increased body of experimental work that quantifies the relative influence of resource availability and nest substrate, and that spans multiple avian taxa.

4. Correlates of deuterium (δD) enrichment in the feathers of adult American kestrels of known origin.

4.1 Abstract

American kestrels (*Falco sparverius*) are experiencing population declines in many locations and it is unknown whether low recruitment and rates of return are due to mortality, poor detection, or dispersal. Stable hydrogen isotope ratios in feathers (δD_f) have been widely used to estimate origins of birds, in some cases providing estimates of breeding and natal dispersal. My goal was to use δD in feathers, grown during breeding, to identify returning and immigrant birds, and quantify breeding and natal dispersal. I used known-origin birds to establish the expected local δD_f but found a higher degree of deuterium enrichment in these individuals relative to the local δD of rainfall (δD_p) than has generally been reported for other birds, and a significant difference between nestling and adult δD_f which complicated the delineation of local and immigrant birds. I subsequently compared the δD of primary feathers and plasma of adult birds, and tested for relationships among the δD of adult feathers and adult mass, structural size, and reproductive effort at the time of growth to explore the cause of deuterium enrichment observed in adult feathers. Adult feathers were significantly more deuterium enriched than plasma. Males that were structurally larger, and females that fledged female nestlings of greater mass exhibited greater deuterium enrichment in their feathers, while males whose mates laid clutches of greater volume had less enriched feathers. I discuss my results within the context of the prevailing hypotheses for deuterium enrichment of raptor feathers and suggest that my data lend indirect support for the evaporative cooling hypothesis.

4.2 Introduction

Studies of avian population dynamics are likely to be incomplete without estimates of breeding and natal dispersal (Negro et al. 1997, Walters 2000). Movement among breeding populations regulates gene flow and resulting population genetic structure, and the extent of among-year dispersal an individual undergoes will influence their familiarity with the local breeding environment (Danchin and Cam 2002, Marr et al. 2002). Both of these components have direct consequences for individual fitness (Doligez and Pärt 2008); therefore, accurate estimates of recruitment rates and the scale of movement among breeding populations are important for determining population status and source-sink dynamics. Nonetheless, for species that are not easily tracked, it can be difficult to determine whether dispersal constitutes small-scale movements to adjacent areas, or large landscape-scale movements. Extrinsic markers are useful for determining return rates to a given study area but when recapture rates are low, it is difficult or impossible to ascertain whether low return rates are due to mortality or emigration (Waser et al. 1994, Rubenstein and Hobson 2004).

A growing number of studies have used stable hydrogen isotopes to estimate the origins of birds. Hydrogen-isotope ratios are the ratio of heavy (deuterium) to light hydrogen ($^2H/^1H$, or δD); precipitation generally becomes more deuterium (^2H) depleted (i.e. more negative δD values) from southeast to northwest in North America and from low to high altitudes (Dansgaard 1964). Consumers incorporate the local isotopic signature of rainfall into their tissues and although error is introduced into the analysis of tissue isotope-ratios by a host of variance generating processes (Wunder and Norris

2008), spatial patterns in isotopic variation are generally reflected in the tissues of higher order organisms (Chamberlain et al. 1997, Hobson and Wassenaar 1997). When synthesized from exogenous sources, tissues that are metabolically inert after growth (claws, feathers) should reflect only the isotopic signature of the food and water being ingested at the time of growth (Hobson and Clark 1992, Hobson and Wassenaar 1997).

In numerous locations throughout North America, American kestrels (*Falco sparverius*, hereafter, "kestrel") are currently undergoing unexplained population declines (Smallwood et al. 2009). Kestrels generally exhibit low recruitment and rates of return to breeding areas (Smallwood and Bird 2002, but see Balgooyen 1976) so within- and among-year movement is therefore difficult to describe. In my study population of kestrels, located in north-central Saskatchewan, kestrels molt their primary flight feathers once per year, beginning during breeding (Smallwood and Bird 2002). Therefore, δD composition of primary feathers collected before molt in the current breeding season should reflect the approximate location of growth in the preceding nesting season. I designed a study to use δD of feathers (δD_f) to estimate breeding and natal dispersal of this population of kestrels. The study was conducted over three years, allowing for the collection of feathers from recaptured birds known to breed in, or hatch from, my location in the previous year. I intended for these known-origin samples to allow me to establish the baseline "local" δD_f, which I expected to show more extensive discrepancies with long-term amount-weighted δD averages of local growing-season precipitation (δD_p) than in other orders of birds (Meehan et al. 2003, Smith and Dufty 2005). The distribution of δD_f derived from my local individuals would allow me to estimate the probability that each unknown-origin individual immigrated to, or bred (or hatched) at my location in the previous breeding season. This would allow much needed estimates of dispersal and recruitment, and provide a basis for the evaluation of the influence of dispersal strategy on reproductive success.

Indeed, the feathers of known-origin adults showed a substantial degree of deuterium enrichment compared with long term precipitation amount-weighted averages of local δD_p as well as the expected value of δD_f derived from a kestrel-specific geospatial predictive model (Hobson et al. 2009; see Results). In the absence of an understanding of the proximate cause and geographic variation of this enrichment I therefore conducted exploratory analyses to shed light on the processes responsible for this phenomenon.

Other studies have shown similar deuterium enrichment in the feathers of adult accipiters (Meehan et al. 2003, Smith and Dufty 2005). Raptors have extended molting periods, which usually overlap with breeding. If physiological processes occur during breeding that influence the δD within the body, these changes would be evident in the δD of tissues such as feathers. Meehan et al. (2003) proposed three non-exclusive hypotheses to explain deuterium enrichment in raptor feathers. The first suggests that if raptors consume migrant avian prey, the isotope ratios incorporated from prey tissue would be reflective of the more positive δD values found in the more southern locations from which these prey originated or passed through. The second poses the possibility that among migratory raptors, new feathers are produced using tissue reserves derived in the non-breeding season as has been shown in adult Anatidae (e.g. Fox et al. 2009). The third hypothesis suggests that body water becomes deuterium-enriched when the lighter form of hydrogen is differentially lost through evaporative water loss (EWL) as a result of the energetic demands of breeding (Wolf and Martinez del Rio 2000, Meehan et al. 2003, McKechnie et al. 2004). Reproduction and molt are both energetically expensive processes (Dietz et al.1992, Weiner 1992) and at such times, when metabolic heat load is high, heat balance is often maintained via EWL (Kvist et al. 1998).

I conducted stable hydrogen isotope analysis on adult feathers and plasma (collected during the period of feather growth), and nestling feathers to examine the cause of deuterium enrichment of feathers in my population. Feather keratin is synthesized from amino acids transported in the blood and upon completion of growth, becomes metabolically inert. Although a general lack of knowledge about tissue-specific discrimination factors for hydrogen isotopes complicates predictions, I expected that if kestrels mobilized non-breeding tissue reserves or consumed migrant prey during feather synthesis, I would find the δD values of plasma (i.e. protein derived from endogenous reserves or migrant prey) to be more similar to feathers of individuals than to the δD values of local precipitation or the feathers of nestlings that are provisioned with local prey. In addition, I examined the relationships between δD_f and measures of body mass and size, and reproduction in the previous year; these are both indicators of conditions with the potential to influence energetic and physiological processes experienced by the birds at the time of feather growth. The activities involved in reproduction elevate metabolism and heat production, and thermal conductance decreases exponentially with increasing body mass (Schleucher and Withers 2001) which may further constrain the capacity for heat dissipation of larger animals in relation to smaller ones. Therefore, I predicted that if deuterium enrichment is a reflection of evaporative cooling that occurs as a function of the energetic rigors of breeding, the degree of enrichment would vary as a function of body mass and/or size and reproductive effort in the preceding breeding (molting) season. I expected a greater degree of enrichment among birds that initiated breeding earlier if feather deuterium enrichment were a function of migrant prey but expected little relationship between size or mass and deuterium enrichment. I made no predictions with respect to endogenous reserves and feather enrichment due to the potential for interaction with a host of other factors, including seasonal interactions influencing individual condition, mate choice, and territory quality.

4.3 Methods

My study area was located near Besnard Lake, Saskatchewan (55°N, 106°W), in the boreal forest. American kestrels are small, migratory falcons, which are secondary cavity-nesters and will readily use nest boxes. I used approximately 255 nest boxes mounted an average of 3.6 m above ground on trees and decommissioned power poles. These were distributed along a network of gravel roads among a variety of forest structure types. Field work was conducted between April and July in 2007 through 2009.

4.3.1 Adult tissue sample collection and body size

In 2007 and 2008 I captured adult kestrels with bal-chatri traps (Berger and Mueller 1959) prior to laying, and in 2007-2009 by hand in the nest box during incubation. All birds captured in 2007 were of unknown origin (i.e. unknown location of breeding / hatching in 2006), whereas in 2008 and 2009 I captured a subsample of kestrels that had been sampled at my study area in the previous years. These recaptured birds comprised my sample of known-origin individuals; the feathers I collected from these birds were grown at my study location in the preceding breeding season. For each bird, I measured the length of the 10th primary feather, central and outer rectrices, and unflattened wing chord to the nearest 0.5mm with a ruler. Tarsus length was measured to the nearest 0.1mm with digital calipers, and mass was obtained to the nearest gram with a spring balance. Feathers were collected for δD analysis by clipping approximately 1.5 cm of feather material from the distal end of 4th primary on the right wing. If this feather was already molted, I collected from the left wing, or clipped the 5th primary if the 4th was molted from both sides. Molt of kestrels begins with the 4th primary and proceeds in both directions (Smallwood and Bird 2002) and at my study area this begins during breeding, usually incubation. I used this first-molted feather to ensure I obtained one that was grown at the location of breeding. Feathers were stored at room temperature in paper envelopes. I collected a small blood sample from the brachial vein of each adult (~ 150μL) with a 27-guage needle and syringe or microcapillary tube. Blood was stored on ice until it was centrifuged; plasma was then drawn off and stored frozen at -20°C until isotope analysis.

To distinguish between the effect of structural size and tissue mass on isotopic composition in the feathers, I first calculated an index of structural size using principal components analysis (PCA; Bortolotti and Iko 1992). The five linear size measurements taken from adults (first capture only) were entered in PCA, conducted separately by year and sex. These analyses explained between 51.70% and 61.84% of the variation, and I used the first component (PC1) as a measure of structural size. Variation in PC1 was largely driven by wing chord, which loaded strongly and positively in all cases (0.81 – 0.90). For males, I then used the residuals from a linear regression of body mass on PC1 ($F_{1,76} = 9.40$, $P = 0.003$) as a measure of body mass not attributable to structural size (residual mass; Dawson and Bortolotti 2000). There was no relationship between mass and PC1 among females in my study area ($F_{1,98} = 0.002$, $P = 0.97$), so I used raw mass for females. I used the mass of birds captured during incubation, except for cases where birds were captured only on bal chatri traps and not subsequently in a nest box. The condition of kestrels can vary during the breeding season (Dawson and Bortolotti 1997); however, I detected no linear or polynomial relationships between capture date or clutch initiation date and raw or residual mass for either sex so did not correct for capture date.

4.3.2 Reproduction

Starting in early May, I visited nest boxes every three to five days to determine clutch initiation dates. Upon clutch completion, I returned to determine clutch size, measure eggs, and capture adults. I measured the length (l) and breadth (b) of each egg to the nearest 0.1mm using digital calipers. Egg measurements were used to calculate total clutch volume, which was obtained by summing the volume of each egg in the nest, given by $0.51*l*b^2$ (Hoyt 1979). The majority of kestrels lay clutches of 4 or 5 eggs in my area (Tella et al. 2000) so I examined clutch volume because it is more variable than clutch size.

I assigned nestling age based on the hatching date of the first-hatched nestling (day 0) in each nest, which was determined by visiting the nest every day, starting 1 to 2 days before the predicted hatch date. Nests were monitored throughout the brood-rearing period and when nestlings were 24 days old I measured length of the 10th primary and mass of each nestling. In 2009, I also clipped the distal 1.5 cm of the 4th primary on the right wing of one male, and one female nestling from each nest. These feathers were stored in paper envelopes until processed in the lab. Kestrels are sexually dimorphic with plumage and size differentiation evident by 12 days of age (Anderson et al. 1993); I calculated the mean mass and length of 10th primary of nestlings in each nest at day 24 for males and females separately. Nestlings fledge between 24 and 30 days of age so I did not visit nests during this period to avoid premature fledging. If no nestlings were found dead in the box 35 to 40 days after hatching, I considered the number of nestlings present in the box at day 24 to be the number successfully fledged.

4.3.3 Isotope preparation and laboratory analysis

Each plasma sample was freeze-dried and stored in small tubes (Wassenaar 2008). Feathers were cleaned of surface oils using an overnight soak and subsequent rinse with a 2:1 chloroform:methanol solvent mixture. To avoid contamination, I cleaned dirty feathers (e.g. nestling feathers caked in feces) with ultra-pure water prior to the solvent rinse. Feathers were then left in a fume hood to air dry for at least 48 hours. I clipped small portions of feather vane from the distal tip of each feather for analysis; for those feathers sampled more than once (among-autorun repeats) I clipped vane material from immediately proximal to the prior clipping, or from the most distal portion on the other side of the rachis. For all tissue types, I loaded 350 ± 10 μg of prepared sample in to silver capsules (Model D2002, Elemental Microanalysis, Okehampton, UK) and then crushed these to remove all air.

Stable hydrogen isotope analyses were conducted at the Stable Isotope Hydrology and Ecology Laboratory at the National Water Research Institute (Environment Canada, Saskatoon, Saskatchewan) using the comparative equilibration approach detailed by

Wassenaar and Hobson (2003); this method uses pre-calibrated keratin reference standards to correct for the portion of exchangeable hydrogen in keratinous tissue. Samples were pyrolized at high temperatures using continuous-flow isotope-ratio mass spectrometry to determine the ratio of non-exchangeable $^2H/^1H$ (deuterium, δD) in the resulting H_2 gas (Wassenaar and Hobson 2003). δD results are expressed in per mil (‰) units relative to Vienna Standard Mean Ocean Water (VSMOW-SLAP) given by the formula:

$$\delta = [(^2H/^1H_{sample}/^2H/^1H_{vsmow}) - 1] \times 1000$$

Measurement repeatability of keratin reference standards is reported as better than ± 2.0‰ (Wassenaar and Hobson 2006). My samples were analyzed for hydrogen-isotope composition in three separate years (2007-2009); known-origin samples (recaptures, grown in 2007 and 2008) were analyzed only in 2008 and 2009. Previous studies have suggested variation in the reproducibility of measurements among auto-runs (Lott and Smith 2006, Smith et al. 2009); therefore, I included repeat samples in each auto-run to account for temporal bias in my isotope measurements. I incorporated seven repeats in each auto-run in 2008 and 2009; the mean difference between auto-run pairs ranged in magnitude from - 0.17 ‰ to 21.17 ‰ and the standard deviation of these differences ranged from 5.25 ‰ to 10.89 ‰ (mean SD: 7.92‰). I conducted reduced major-axis (RMA) regression between repeats from one arbitrarily chosen auto-run and each additional set of auto-run repeats. These correction equations allowed me to normalize δD values to one common auto-run. My repeat samples do not represent true replicates because δD can vary along the length of feathers (Smith et al. 2008); however, all feather samples, including repeats, were taken from the distal 1.5 cm of the feather to minimize this possibility. I did not include replicates in 2007 samples (grown in 2006), so I could not correct these to one auto-run; therefore, only known-origin samples (grown in 2007 and later) were corrected to the same run.

I obtained the predicted mean annual and mean growing season precipitation amount-weighted δD of rainfall (δD_p) for my study site from the Bowen and Revenaugh (2003) and Bowen et al. (2005) spatial models (Bowen 2010). For this I used coordinates located near the centre of the study area (55° 12.9248'N, 106° 03.0807'W). Growing season encompasses those months with a mean temperature greater than 0°C. Expected δD_f of kestrels at my location was obtained from the kestrel-specific surface in Hobson et al. (2009), which depicts the geographic distribution of expected δD_f from a RMA regression between known-origin feathers of juvenile kestrels (Lott and Smith 2006) and the GIS model of expected growing season δD_p (Bowen et al. 2005).

4.3.4 Statistical analyses

The raw δD_f values from all birds (known and unknown origin) were visually examined prior to analysis. I plotted the autorun-normalized values for the δD_f of adult known-local birds (recaptures in 2008 and 2009) and nestling birds of 2009, and the δD of the plasma samples against the mean annual and mean growing season precipitation amount-weighted δD_p and the kestrel-specific expected δD_f for my area. I did not test for statistical differences between the δD_f of adults and nestlings because these feathers were grown in different years. I used a paired t-test to examine differences between δD of feather and plasma samples collected from the same individual; plasma was sampled in the year feathers were grown (the year preceding feather collection). All subsequent analyses examining relationships between δD_f and adult characteristics were carried out with only those birds that were known to be caught at my study area in the previous year (body size and mass) and were known to breed there in the previous year (reproduction). For each of these analyses, I used the morphological measurements and reproductive traits collected in the year prior to feather collection, as these were the conditions experienced during the time of feather synthesis.

To determine whether all data met distributional assumptions, I examined residual plots, and tested for normality using Shapiro-Wilk's test; I assessed equality of group variance using Levene's test. Males and females were analyzed separately; I used a General Linear Model to test for relationships between δD_f and structural size, and residual mass of known-local males. Structural size (PC1), residual mass and year were fixed factors and I included terms for interactions between year and both structural size and residual mass. A number of females were caught in multiple years, so I included female identity as a random factor in a Linear Mixed Model to control for the non-independence of these observations. Structural size (PC1), raw mass, and year were fixed factors and I included terms for interactions between year and both structural size and mass. For both males and females, terms were sequentially removed where $P \geq 0.10$. I used all known-local birds that were captured on the study area at any time during the previous breeding season.

To explore possible relationships between δD_f and reproductive effort during the time of feather growth, I performed Pearson's correlations between δD_f and breeding variables associated with each adult in the previous year that may represent some measure of the amount of energy expended during breeding. These included clutch initiation date, total clutch volume, sex ratio of broods at day 24, number of young fledged at each nest, mean mass per nest of male and female nestlings at day 24, and mean length of the 10th primary of males and females in each nest at day 24. I chose correlations because of the exploratory nature of this study and because the likely co-variation of reproductive variables with other factors (e.g. resource availability, adult quality) may render some models too complex for the scope of my data

Results were considered significant at $P \leq 0.05$ and means are presented ± 1SE unless otherwise indicated. All statistical analyses were performed using SPSS 16 (SPSS Inc., Somers, New York, USA).

4.4 Results

4.4.1 Tissue-isotope distribution

For all adult feathers sampled in 2007 and 2008, the modal δD_f was -62‰ (min. = -134‰, max. = -20‰, SD = 26.20‰). The frequency distribution of adult kestrel δD_f was bimodal, with a break at approximately -90‰ (Fig. 4.1). The sub-sample of known-origin kestrels (those that were sampled at my study area in consecutive years) showed a mean δD_f (-50.76‰) well above both the mean annual (-129.65‰), and mean growing season (-114.69‰) δD_p and expected δD_f (-143.06; based on Hobson et al. 2009) for this location (Fig. 4.2). In contrast, the mean δD_f of nestling kestrels (-111.3‰) was significantly less enriched relative to the above expected values (mean annual and mean growing season δD_p, and expected δD_f);

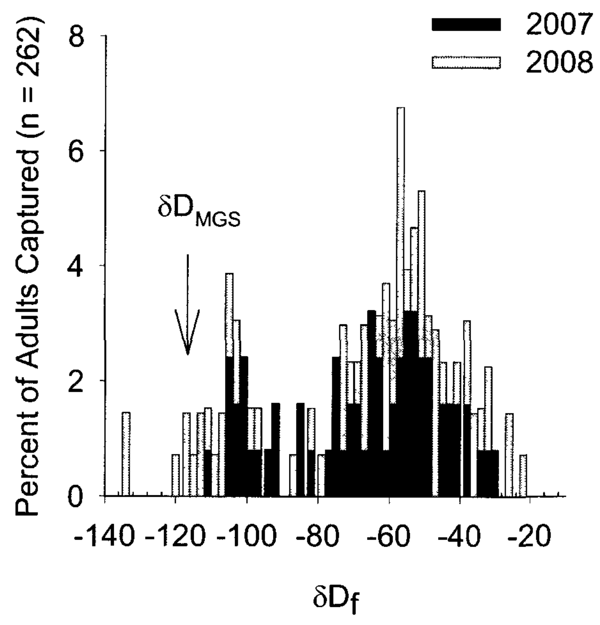

Figure 4.1 Frequency distribution of raw stable-hydrogen isotope values of the primary flight feathers (δD_f) of all American kestrels (*n* = 262) sampled in 2007 and 2008. Precipitation amount-weighted mean growing season δD (δD_{MGS}) is indicated with an arrow.

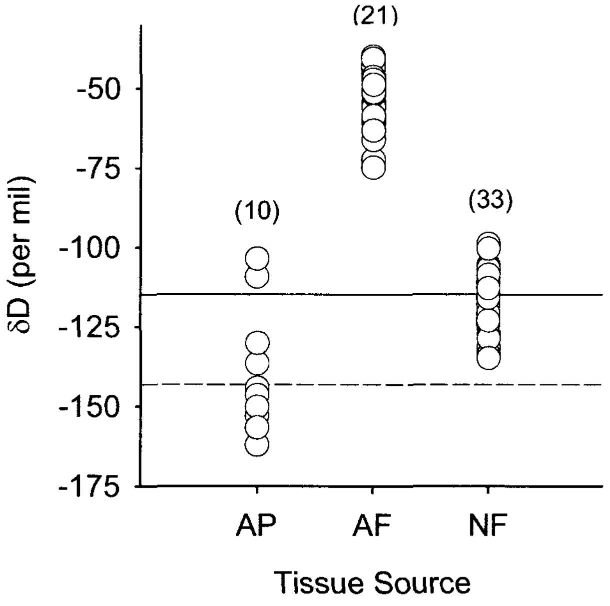

Figure 4.2 Stable-hydrogen isotope values (δD) of the primary flight feathers (AF) and plasma (AP) of known-location, recaptured adult American kestrels sampled in 2008 and 2009, and the feathers of nestling kestrels (NF) sampled in 2009. All isotope values are normalized to a common auto-run. Reference lines indicate the mean precipitation weighted-average growing season δD_p (solid line; Bowen et al. 2005) and expected δD_f derived from a GIS-based model of known-origin juvenile kestrel feathers (broken line; Hobson et al. 2009) for my study area. Sample sizes are in brackets above each set of observations.

nestling and adult δD_f distributions did not overlap (Fig. 4.2). Among the adults from which I analyzed both plasma and feathers, δD_f was significantly more positive than plasma (paired t-test: $t_9 = 14.03$, $P < 0.001$); the mean difference was 93.41‰ ± 6.66 SE (Fig. 4.2).

4.4.2 Deuterium enrichment, size, and mass

I found no significant relationship between δD_f and either female size (PC1: $F_{1,11\ 8} = 0.34$, $P = 0.57$) or mass ($F_{1,11\ 90} = 2.30$, $P = 0.64$), but there was a significant year effect ($F_{1,6\ 25} = 11.36$, $P = 0.01$). Nonetheless, exploratory analyses showed a negative correlation between δD_f and mass in 2008 ($r = -0.63$) which was non-significant ($P = 0.18$) but perhaps notable in light of small sample size in that instance ($n = 6$). For males, there was a significant effect of size ($F_{1,12} = 11.58$, $P = 0.005$, Fig. 4.3) suggesting that larger-bodied males experienced greater deuterium enrichment than smaller males. There was no effect of residual mass ($P = 0.27$) or year ($P = 0.97$), so I removed these factors from the model.

4.4.3 Deuterium enrichment and reproduction

Correlation analysis showed a negative relationship between clutch volume and the δD_f of male parents (Table 4.1) suggesting that the feathers of males whose mates laid larger clutch volumes were less deuterium enriched than those whose mates laid smaller clutches. In addition, the correlation coefficient between length of 10th primary of male nestlings and δD_f of male parents was -0.78; this relationship was not significant ($P = 0.07$), but sample size was small ($n = 6$). Among the variables I tested, only the mean

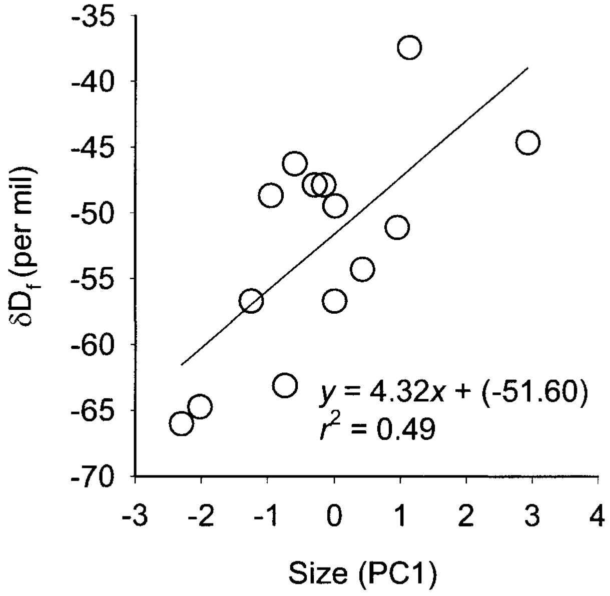

Figure 4.3 The relationship between structural size (PC1) and δD$_f$ of male American kestrels originating at my study location near Besnard Lake, Saskatchewan.

Table 4.1. Pearson's correlations for the relationship between stable hydrogen isotope ratio of the 4th primary flight feathers of adult American kestrels (δD_f) and reproduction in the year the feather was grown.

Variable	Male			Female		
	r	*P*	*n*	*r*	*P*	*n*
Clutch Initiation Date	-0.37	0.47	6	0.06	0.86	12
Clutch Volume	-0.84	0.04	6	0.07	0.81	13
Sex Ratio	0.40	0.43	6	-0.03	0.94	11
Number of Young Fledged	-0.58	0.23	6	0.31	0.30	13
Mean mass of female nestlings	0.53	0.36	5	0.82	0.01	8
Mean mass of male nestlings	0.21	0.69	6	0.29	0.41	10
Mean 10th primary length of female nestlings	0.42	0.48	5	-0.25	0.56	8
Mean 10th primary length of male nestlings	-0.78	0.07	6	-0.32	0.37	10

mass of female nestlings at day 24 showed a significant positive relationship with δD_f of adult females (Table 4.1), indicating that adult females that raised nestling females with a higher fledging mass experienced greater deuterium enrichment.

4.5 Discussion

4.5.1 δD_f and estimating dispersal

The feathers of adult kestrels of known breeding origin showed a high degree of deuterium enrichment relative to weighted average growing season δD_p (Bowen et al. 2005) and expected δD_f based on a continent-wide kestrel δD_f isoscape (Lott and Smith 2006, Hobson et al. 2009) that supports notions that increased work during molting can result in δD_f enrichment Meehan et al. (2003) and Smith and Dufty (2005). These results provide evidence that this phenomenon is not limited to accipiters, but extends to falcons, and perhaps to other birds with similar life histories. In the absence of the knowledge that each of these individuals bred at my study area in the previous year, the δD_f values of my sub-sample (-74.73 to -22.95‰) of known local kestrels would indicate much more southern and/or eastern origins. My interpretation of the greater data set would likely have been that my sampled population is comprised both of site-fidelic birds and birds that undergo variable degrees of breeding or natal dispersal (immigrants). Nestling values were less deuterium enriched relative to both expected δD_p and δD_f. The distribution of δD_f of known-origin nestlings versus adults suggests that the bimodal distribution of δD_f of all sampled individuals (Fig. 4.1) is likely a function of second year (values less than -90‰) and after second-year (values above -90‰) birds in the sample rather than variation in breeding provenance. Both GIS models of expected δD_f (Lott and Smith

2006, Hobson et al. 2009) were constructed using known-origin juvenile feathers, so given the difference I observed between nestling and adult δD_f it is not surprising that my known-origin adult δD_f values were deuterium enriched at my site relative to that predicted from Hobson et al. (2009). Although the use of known-origin feather samples allowed me to establish a "local" δD_f distribution, I was unable to use this to estimate the probability that unknown-origin birds were either local or outside recruits due to the difference between nestling and adult known δD_f values. Extensive observation at my study area through time (G.R. Bortolotti, R.D. Dawson and J.L. Greenwood, *unpubl. data)* has shown that adult birds cannot be reliably aged. Therefore, I would be unable to determine whether unknown-origin individuals should be compared to my local nestling or adult distributions.

My results reinforce assertions (Meehan et al. 2003, Smith and Dufty 2005) that until such time as the physiological underpinnings of deuterium enrichment in adult raptor feathers are understood, hydrogen isotopes should be used with caution to estimate origins in raptors. Hobson et al. (2009) explored the utility of using the relationship between $\delta^{18}O$ and δD to identify kestrel feathers that were unreliable indicators of origin, and showed that those feathers with δD above approximately -20‰ departed from the generally linear relationship with $\delta^{18}O$. However, their study did not sample known-origin birds, so although the authors recommend using $\delta^{18}O$ as a tool for eliminating birds with enriched values from interpretation, it is yet to be tested whether the departure from a linear $\delta^{18}O$ to δD relationship is directly related to deuterium enrichment relative to local rainfall and whether this would be reliable for all sampled populations.

4.5.2 Tissue sources and deuterium enrichment

Together, the δD values of adult plasma and feathers neither support nor disprove Meehan et al.'s (2003) first or second hypothesis as explanations for deuterium enrichment in feathers of adult kestrels. Tissue-specific discrimination occurs with other stable isotopes (e.g. DeMots et al. 2010) and may occur with δD also. Nonetheless, plasma values were, on average, 93.41‰ more depleted than feathers of the same individuals, and were more depleted than long-term weighted averages of both mean annual and mean growing season δD_p. If kestrels were mobilizing endogenous tissue reserves or consuming migrant prey consisting of more southern δD values, it is possible that the plasma of adults would be more positive than the δD of long-term precipitation averages. Furthermore, birds comprise a smaller part of the breeding season diet of kestrels at my study location than small mammals, insects, and frogs combined (Bortolotti et al. 2000). Experiments designed to examine tissue-specific discrimination in this species would undoubtedly clarify predictions associated with these two hypotheses.

Unfortunately, comparisons between plasma and feathers were less useful for evaluating the evaporative cooling hypothesis. Preparation for isotopic analysis requires the removal of water from the plasma. Water-bound hydrogen in plasma is the most likely source of light hydrogen lost to evaporation (Schoeller et al. 1986) and body water supplies approximately 26 to 32 % of non-exchangeable hydrogen in feather keratin (Hobson et al. 1999). It is unknown whether the deuterium enrichment of this water as a result of evaporative cooling would be sufficient to produce such enriched values in feathers, but given my results, warrants further examination.

4.5.3 δD_f relationships

My results relating deuterium enrichment of adult feathers to body mass and size, and reproduction are difficult to interpret in the context of Meehan et al.'s (2003) first and second hypotheses. A host of factors, including but not limited to, the relative abundance of various prey sources, annual weather events that may influence migrant prey or the behaviour of kestrels, and the influence of carry over effects from the previous season on body condition would be necessary to better evaluate these hypotheses. My results concerning adult mass and size, and reproduction do, however, provide indirect support for the evaporative cooling hypothesis.

Birds tend to have higher basal metabolic rates than similar-sized mammals (Arieli et al. 2002) and the majority of metabolic energy is converted to heat, rather than mechanical work (St. Laurent and Larochelle 1994, Engel et al. 2006). Individuals can facilitate dry heat dissipation through various means, but as the ambient temperature increases, conditions for this become less favorable as the gradient between body temperature and air temperature decreases (Engel et al. 2006). Numerous studies have found that above a threshold ambient temperature evaporative water loss (EWL) increases linearly with temperature (Schleucher et al. 1991, Kvist et al 1998, Bakken et al. 2002, Cooper and Tessaman, 2004, Engel et al. 2006). Betini et al. (2009) found maximum ambient temperature in the nest box predicted deuterium enrichment in the blood of nestling tree swallows (*Tachycineta bicolor*), which may be illustrative of this relationship between EWL and ambient temperature.

Evaporation can occur from the respiratory tract, eyes, and cutaneous body surfaces. Panting is a well-documented behavior for respiratory water evaporation

(RWE), but the extensive contractions of the respiratory muscles required to do so are energetically expensive, creating more heat (Arieli et al. 2002). In heat-acclimated birds, cutaneous water evaporation (CWE) is particularly important and is enhanced due to an increase in microvessel permeability as a function of the activation of the adrenergic signal transduction pathway (Arieli et al. 1999, Arieli et al. 2002, Ophir et al. 2004). Although the extent to which other birds utilize CWE is not well-understood, this mode of heat dissipation saves energy and reduces heat shock (Schleucher et al. 1991, McKechnie and Wolf 2004) in relation to RWE. It is unclear whether either of these processes would contribute to heat balance in kestrels. I have observed panting to occur while kestrels are perched, but do not know the degree to which they may open the bill during flight to facilitate respiratory evaporation. Although the cere and lores may provide enhanced surface area for CWE, it is unknown whether kestrels are adapted to utilize this mode of evaporation as extensively as some desert-dwelling, heat-acclimated birds do (Arieli et al. 1999).

4.5.4 Body mass and size

My results indicate that males of larger structural size are subject to a higher degree of deuterium enrichment than smaller males (Fig. 4.3). Betini et al. (2009) similarly found that body size, represented by tarsus length, positively influenced deuterium enrichment in the blood of nestling tree swallows. I detected no significant relationship between either size or mass and δD_f in females. Metabolism is proportional to mass; smaller birds tend to have more moderate metabolism (Bakken et al. 2002), generating less heat. Bakken et al. (2002) showed that EWL in scolopacid chicks was proportional to mass and that the positive relationship between EWL and air temperature was dependent on mass, likely because the effectiveness of dry heat transfer is dependent on size. Larger kestrels may utilize EWL to a greater extent because higher energy requirements produce more heat which needs to be dissipated. In addition, CWE is proportional to surface area, which in turn is proportional to mass (Bakken et al. 2002), so larger kestrels with greater overall surfaces from which to facilitate EWL may be subject to greater deuterium enrichment. Alternately, relative surface area decreases with greater mass, and thermal conductance decreases exponentially with increasing mass (Schleucher and Withers 2001), so larger bodied birds may have a lower capacity for passive heat dissipation thus relying more substantially on EWL. In either case, if a significant proportion of EWL is respiratory, the energy required to pant would itself produce more heat (Arieli et al. 2002), essentially creating a positive feedback loop such that larger birds would consistently create and dissipate more heat and lose more depleted hydrogen via EWL.

4.5.5 Reproductive effort

I found a negative correlation between the clutch volume of a pair and the δD_f of the male, suggesting that males whose females lay clutches of lower volume undergo greater deuterium enrichment. Although they are not subject to the burden of producing eggs, male kestrels provide a considerable amount of food for their mate during pre-laying and incubation, and for the nestlings until approximately 10 days of age, after which more of this responsibility is taken up by the female (Balgooyen 1976). Although it is the female that ultimately produces eggs, clutch volume is likely influenced by the amount of food she receives from her mate prior to and during laying. Kestrels at my study area have been shown to increase the size of eggs in response to food supplementation (Wiebe and Bortolotti 1995) and studies of Eurasian kestrels (*F. tinnunculus*) have shown that variation in food availability drives phenotypic plasticity in clutch size (Korpimäki and Wiehn 1998). If larger males must devote more time to fulfilling their own energy demands, this may translate in to less time available for provisioning females and a smaller clutch volume. My finding that males of larger size undergo greater deuterium enrichment could therefore account for the negative relationship between clutch volume and enrichment. This seems unlikely, however, because I found no evidence that larger or heavier males were mated with females that laid clutches of smaller volume either within the sample of known origin birds (PC1: $r = 0.20$, $P = 0.74$, $n = 5$; Residual Mass: $r = -0.02$, $P = 0.97$, $n = 5$) or among all nests at my study site (e.g. 2008 [PC1: $r = 0.06$, $P = 0.72$, $n = 44$; Residual Mass: $r = 0.11$, $P = 0.48$, $n = 44$]). Alternately, males may realize lower clutch volume as a function of the costs associated with lower quality territories, such as increased time spent avoiding predation, or lower food availability. If these males work harder to provide food for their mates, thereby creating more heat and decreasing the gradient between body and ambient temperature, they may also undergo a greater degree of heat production, EWL, and hence deuterium enrichment.

If all else were equal, producing larger nestlings would require greater energy input and heat production for the parent, although many individually variable traits could uncouple this relationship. Engel et al. (2006) found that regardless of the ambient temperature or speed of flight, a net water loss consistently occurred during the flight of rose-colored starlings (*Sturnus roseus*). Although falcons employ different modes of flight than starlings, and the number of flights will depend on the type of prey being delivered (biomass per trip), if greater provisioning effort requires more flights to and from the nest, this will likely result in greater EWL. I propose that this may be related to the positive correlation I observed between adult female δD_f enrichment and nestling female mass. Finally, if as suggested by the heat dissipation limit theory, energy expenditure is limited not by energy supply, but by an individual's ability to dissipate metabolic heat (Speakman and Krol 2010), then adults with plentiful access to resources may be at the upper limit of their ability to dissipate heat, thereby exhibiting higher rates of EWL; the availability of these resources may be reflected in nestlings that fledge at larger sizes.

4.5.6 Conclusions

I have shown that substantial deuterium enrichment occurs in adult kestrels in relation to the δD of plasma, nestling feathers, and local precipitation, and that the degree of enrichment is associated with measures of size and reproductive effort at the time of feather growth. These results lend support to the evaporative cooling hypothesis, although I suspect that low statistical power prevented the detection of further relevant relationships with some of the variables that I tested. I did not examine some of the factors that are likely to interact with those tested here to influence deuterium enrichment. For example, the degree of EWL is dependent on air temperature, and the water vapor deficit between body surfaces and surrounding air (Engel et al. 2006), neither of which I was able to quantify. In addition, I did not account for the proportion of time spent incubating by each sex, and pre-existing conditions which might influence the energy budgets of adults. Finally, further studies should isolate the body water contained in plasma to compare δD in this source with that of both non-water plasma and feathers.

5. General Synthesis

Data derived from both long-term monitoring programs and individual research populations show that American kestrels are exhibiting population decline in much, though not all, of their North American range (Smallwood et al. 2009a). The causal mechanisms for this phenomenon are as yet unknown. West Nile virus, increased predator populations, declines in breeding habitat, and deleterious conditions encountered during migration and wintering have all been suggested as potential causes but thus far there are few data and little evidence to support any of these ideas (Smallwood et al. 2009a). This is clearly a problem that requires information about how individuals move within and among years, how populations interact, and the causes and consequences of such decisions and processes. Detecting these movements and interactions, which can generally be described as dispersal and migration (Greenwood and Harvey 1982), is necessary for modelling population and metapopulation processes (Lawton and May 1983, Robinson et al. 1995), understanding the evolution of life histories (Sillett and Holmes 2002) and tracking disease trajectories (Rappole et al. 2000).

In an attempt to describe breeding and natal dispersal, I used stable hydrogen isotopes in the feathers of American kestrels to estimate the location of growth in the previous breeding season. Although there is not generally a 1:1 relationship between hydrogen ratios in the environment and those found in avian tissues (Bowen et al. 2005) some studies have, to varying degrees, quantified and accounted for variability in tissue isotope ratios (e.g. Hobson et al. 2009, Sellick et al. 2009). Using a sub-sample of known-origin birds, I found a high degree of deuterium enrichment in feather hydrogen of adults relative to the average δD in the feathers of nestlings and in precipitation at my study site.

With little understanding of the proximate mechanism responsible for this enrichment, hydrogen isotopes were an imprecise tool to estimate origins of the larger sample of individuals of unknown age and unknown provenance.

Whether or not a bird exhibits among-year dispersal will influence the extent of the prior knowledge they possess about local resources, threats, and conditions in their chosen breeding site (Danchin and Cam 2002, Marr et al. 2002), which will be mediated by the degree of environmental heterogeneity in space and time in that location (Bowler and Benton 2005). Furthermore, the extent of dispersal influences a population's genetic structure (Marr et al. 2002). Exclusive of isotopic methods, most current methods of tracking movement of small animals, including uniquely marking individuals (banding), radio telemetry and attaching geolocator devices, require that individuals be recaptured or at least closely followed to either identify the individual or download the data. Kestrels at my study area generally exhibit low rates of recapture among years (Bortolotti et al. 2002) so these methods are relatively ineffective for determining movement and mortality in this population. My results highlight the need for more effective tools to do so. Satellite transmitters offer promising solutions for tracking birds at high resolution without the need to recapture them to obtain the data; however, substantial technical hurdles remain. Currently, satellite transmitters are too large for use on most birds and require further miniaturization (Wikelski et al. 2007). The International Cooperation for Animal Research Using Space initiative proposes a very sensitive low orbit satellite receiver to track signals from transmitters small enough to be fitted on small birds and insects, but the realization of this project may be years away (Wikelski et al. 2007).

Although my study was unable to determine such broad-scale settlement decisions as among-year dispersal, I was able to evaluate the settlement decisions of kestrels at the territory and nest-site scales. Secondary cavity-nesters do not excavate cavities and are therefore limited to those previously created by other primary-cavity nesting species. So although these birds should seek to minimize the costs of the breeding site they choose, they must do so within the confines of available nest cavities. Contrary to prediction, I found that the abundance of prey in the immediate vicinity of nest boxes did not influence nest-site selection, nor did manipulations of the perception of the risk of nest predation. Nonetheless, the natural abundance of nest predators did influence nest-site selection, as did other structural breeding-site features (Chapter 3). Nest sites located in disturbed habitats including recently harvested forests and those previously burned by a forest fire were more likely to be chosen, indicating a preferential association with disturbed habitats (Chapter 2). Furthermore, the higher index of body condition of those males that settled in the burned area is suggestive that the some aspect of the territories in this area are of higher quality or that males in better condition are out-competing lower quality males for territories in this area. As discussed in Chapters 2 and 3, there are numerous possibilities that may explain these preferences including interspecific interactions and components of the structural landscape that favourably mediate parental behaviour for maximum reproductive benefit. These mechanisms certainly warrant further research but provide some insight into the specific features of territories and nest sites which influence the reproductive decisions of kestrels at my study area.

The benefits of the settlement decisions that I observed were evident in light of subsequent reproductive success. In some cases, however, kestrels did not show a significant preference for certain conditions but rather adjusted reproductive decisions to conditions encountered at the nest site once chosen. For example, although food supply has been shown to influence reproductive outcomes (Wiebe and Bortolotti 1992, 1995, Wiehn and Korpimäki 1997, Martinez-Padilla and Fargallo 2007) and parental behaviour (Dawson and Bortolotti 2002) of both American and Eurasian kestrels, my results showed that over eight years, kestrels did not chose nest boxes according to the prey abundance in the immediate vicinity but they did adjust the timing of breeding and clutch size in relation to prey abundance (Chapter 2). Further, although experimentally increased risk of nest predation did not influence nest-site selection, kestrels did adjust the timing of breeding and clutch size in response to this experiment, and although analyses of adult incubation behaviour were inconclusive, hatching success at experimental nests was lower, which corresponded with longer incubation periods (Chapter 3). Male kestrels establish territories, and during or after mate selection, females chose from among the available nest sites on the male's territory (Balgooyen 1976). As secondary cavity nesters, the number of nest sites (holes, boxes) in a territory available for breeding is limited and in accordance with this limitation, females may contend with a relatively inferior nest-hole for the benefit of a territory and/or mate that is, on balance, of higher quality than others encountered during her search for a nest site. Whether or not this is the case, if nest sites are sufficiently limited, females may be forced to initiate breeding in a somewhat inferior nest site rather than forgo breeding altogether (Nilsson 1984). If so, breeding effort and parental effort should be adjusted to fit the conditions encountered at this site for maximum fitness benefit. Indeed, my results showed that while certain ecological factors may not be sufficient to affect the choice of a nest site, kestrels may respond to such factors with respect to decisions concerning reproductive investment.

Taken together my studies highlight the complexity of the constraints acting on reproduction for this species. Although nest predation has long been known to be an important driver of reproductive success (e.g. Ricklefs 1969) there is only more recently a growing body of work examining strategies to minimize the cost of nest predation (Lima 2009). If the response of kestrels in this study is representative of other secondary cavity-nesters, then decisions concerning mitigation of predation risk are likely balanced against the availability of appropriate nest sites. This study also provides an indication that parental behaviour and ensuing ecological interactions and reproductive success are mediated by structural habitat features which, at my study location, vary spatially and temporally. Kestrels breed in a broad cross-section of geographies and landscapes, and the relative importance of these habitat mediated interactions will likely vary among these. Finally, current reproduction is thought to come at the cost of future reproduction and survival as a function of limitations of internal energy reserves (Stearns 1992, Harshman and Zera 2007). The suggestion that the isotopic discrepancy between environment and the feathers of kestrels is a function of heat stress raises the question of whether heat production is a benign product of breeding or whether there is a physiological cost involved. Some birds may be limited not by energy acquisition, but by the ability to dissipate the heat created from energy inputs (Speakman and Krol 2010). Among others, a key prediction of this hypothesis is that larger-bodied animals are constrained to a greater degree due to their relatively limited ability to elevate their metabolic rate (Speakman and Krol 2010). If evaporative cooling as a function of thermal stress is a cause of deuterium enrichment, my result that larger-bodied males exhibit a greater degree of deuterium enrichment provides indirect support for the aforementioned prediction. The finding that females who raise heavier female offspring exhibited greater deuterium enrichment may also indicate that adults are energetically constrained by the ability to dissipate heat during reproduction. Habitat quality also likely interacts with work and energy production in this context. Adults on poorer quality territories may be required to work harder to successfully produce young, and subsequently suffer physiological costs, but while adults on higher quality territories may enjoy access to more plentiful food, they may nonetheless suffer physiological costs if they are at the upper limit of their ability to dissipate the resulting metabolic heat. The difference, however, may be that the young produced at the higher quality site are more robust. While these hypotheses are untested in this thesis, the marked degree of deuterium enrichment in adult feathers and the relationships between enrichment and size, and enrichment and reproduction indicate the likelihood of substantial but poorly understood physiological trade-offs that occur for adult kestrels during reproduction.

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