NEST CHARACTERISTICS, BREEDING DISPERSAL, AND NEST DEFENCE

BEHAVIOUR OF NORTHERN FLICKERS IN RELATION TO NEST PREDATION

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ABSTRACT

I studied nest characteristics, breeding dispersal, and nest defence behaviour of Northern Flickers (*Colaptes auratus*, hereafter flickers) in central interior British Columbia with respect to nest predation. My research focused on three questions: (1) Are there nest characteristics associated with the risk of nest predation and nest loss to European Starlings (*Sturnus vulgaris*)? (2) Does nest predation influence breeding dispersal? (3) Do parental attributes influence nest defence behaviour?

An examination of flicker nest-site characteristics at five spatial scales revealed that nests were safer from mammalian predators (N=81) when they were higher, concealed by vegetation, farther from continuous coniferous forest blocks, and contained fewer conifers within the nesting clump. Proximity to conifers increased predation risk, but nests safe from competitors (N=18) were closer to coniferous forest blocks and contained a higher percentage of conifers in the nesting clump. Flickers face a trade-off between being safe from predators and safe from competitors.

Nesting success did not influence between-year breeding dispersal by 159 male or 76 female flickers. Because nests and forest clumps were not predictably safe from predators, benefits of dispersing likely outweigh costs. Other factors such as mate-switching, nest ectoparasites, and a fluctuating food source may play larger roles in dispersal than nest predation. Within years, 73% of pairs switched nest sites after their first attempt failed due to predation (N=37); however, there was no reproductive advantage for these pairs compared to pairs that remained at their original nest. Stressful encounters with predators involving nest defence may trigger dispersal, although it seems to offer no greater nest success. Of 24 flicker pairs presented with a

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control model before egg-laying, 3 pairs abandoned their nest, whereas 4 out of 24 pairs presented with a squirrel model abandoned their nest. This suggests that a one-time encounter with a nest predator is not a sufficient deterrent against continued nesting. Rather, costs of finding and excavating or renovating a new cavity may cause individuals to tolerate some risk in nesting at a location with an active predator.

In experimental trials (N=94), intensity of nest defence behaviour against a model predator was not related to the sex, age, body size, and body condition of the defending adult(s). The sexes may have behaved similarly because they are similar in size and have similar survival patterns. Costs and benefits of nest defence for flickers of different ages may also be equal because flickers are relatively short-lived and their survival rate is not linked with age. Brood size of the defending adult was also unrelated to the intensity of nest defence. If flickers have adjusted their clutch size in relation to the number of young for which they can optimally provide care, then no effects of brood size on nest defence behaviour should be recorded, as was the case here.

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CHAPTER 1
GENERAL INTRODUCTION

1.1 Introduction

Nest predation is a major cause of nest failure for birds, and occurs across a wide

range of taxa, habitats, and geographic locations (Martin 1993). Nest predation

typically results in complete clutch loss, thereby lowering parental fitness (Li and

Martin 1991). Natural selection should favour birds that choose safe nest sites (passive

nest defence), employ nest defence behaviours (active nest defence) or use a

combination thereof (Filliater et al. 1994; Cresswell 1997; Larivière and Messier 1998).

In the short term, nest predation may vary spatially or temporally; however, choice of

nest sites and behavioural decisions influenced by natural selection should reflect long-

term optima (Martin 1995; Badyaev and Faust 1996; Clark and Shutler 1999).

Many avian species are distributed non-randomly throughout a habitat as a result

of nest-selection strategies, and predation is frequently cited as one of the main factors

that influences nest placement (Chase 2002). A comparison of successful versus

depredated nest sites allows one to determine whether predation could be the process

behind a non-random pattern of nest selection (Clark and Shutler 1999). If

characteristics of successful and depredated nests differ in one direction from mean

values, then directional selection can occur. Stabilizing selection occurs when nest sites

with characteristics farther from mean values have relatively high predation rates or can

result through oscillating selection, favouring sites with intermediate characteristics.

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Disruptive selection favours those nests with characteristics that are at extreme ends of the habitat gradient. When the type of selection is known, a prediction can be made regarding how nest characteristics should change over generations in response to nest predation.

Predation can also affect nest selection on a temporal scale either within or between years (Greenwood and Harvey 1982). Predators may remember nest locations and depredate nests consistently, selecting for new nests to be built and old ones abandoned (Sonerud 1985a; Korpimäki 1987). Experience with a predator in past or current breeding attempts may lead to abandonment of nest sites with a history of predation (Dow and Fredga 1985). Conversely, fidelity to nest sites that are predator free either in the short or long term should be a reasonable strategy for nesting birds trying to maximize fitness (Greenwood and Harvey 1982).

If nest placement to avoid predation is unsuccessful, then birds must actively defend their nest against a predator. Active defence probably places the parent at significant risk, but it can effectively deter nest predators (Greig-Smith 1982). Economic models are used to describe individual variation in nest defence, where benefits of defensive actions must outweigh costs (Montgomerie and Weatherhead 1988).

Cavity-nesting species such as woodpeckers have evolved one of the most effective nesting strategies to reduce predation. Compared to open-cup nesting species, cavity nesters experience significantly lower rates of nest predation (Martin and Li 1992, but see Sonerud 1985b). Primary cavity excavators may also have lower nest predation rates than secondary cavity nesters (Martin and Li 1992). Although cavities

are relatively safe compared to other types of nests, predation is usually the greatest source of clutch or brood loss and therefore should influence nest selection and breeding dispersal. Nest defence should also be employed by cavity nesters even though they may rely upon the cryptic or inaccessible nature of their nests to avoid predators (Nilsson 1984).

My objectives were to examine the association between nest predation risk and attributes of cavity nests within and between years (passive defence), and to examine individual variation in active defence behaviour of the Northern Flicker (*Colaptes auratus*). In Chapter 2, I identify attributes of flicker nest sites associated with the probability of nest predation by small mammals and attributes associated with nest loss caused by an avian competitor. I also examine temporal patterns of these two sources of nest loss, as well as nest loss in general. In Chapter 3, I examine the effect of nest predation on between- and within-year breeding dispersal. Finally, Chapter 4 details the influences of age, sex, brood size, body size, and body condition on nest defence behaviour of flickers presented with a model predator.

1.2 Study Species

The Northern Flicker is a common woodpecker found in most forested areas of North America (Moore 1995). Two of the five North American subspecies, Yellow-shafted (*C. a. auratus*) and Red-shafted flickers (*C. a. cafer*) occur in Western Canada, and form a hybrid zone parallel to the Rocky Mountains (Moore 1995). Males and females are sexually dimorphic with respect to plumage coloration, and males are approximately 2-3% larger than females (Wiebe 2000). Excavation of a suitable nest cavity (it is not known which sex chooses the nest location) occurs in early May, and

clutches are laid shortly after excavation or renovation of the cavity is complete (Moore 1995). Clutch sizes range from 4-13, with a mean clutch size of 6.5 (Wiebe 2001). Both parents care for the altricial young until they fledge approximately 27 days after hatching (Short 1982).

1.3 Study Site

The study site near Riske Creek, British Columbia (51°52'N, 122°21'W) encompasses approximately 100 km² with 90-120 pairs of flickers nesting there each year. Habitats on the site are patchy and variable: grasslands are preferred for foraging, patches of trembling aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) are used for nesting, and continuous forests of Douglas-fir (*Pseudotsuga menziesii*) and hybrid spruce (*Picea engelmannii* x *glauca*) also occur.

Major predators of cavity nests in the area include red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), deer mice (*Peromyscus maniculatus*), and long-tailed weasel (*Mustela frenata*), with predation by black bear (*Ursus americanus*) and pine marten (*Martes americana*) occurring less frequently (Walters and Miller 2001). Nest evictions by European Starlings (*Sturnus vulgaris*) and occasionally Tree Swallows (*Tachycineta bicolor*) also occur.

1.4 Locating and Measuring Nest Sites

Each year since 1998, the area has been surveyed in spring to check old cavities for breeding pairs and to search for newly excavated cavities. Data on flicker nesting was collected by K.L. Wiebe before 2003, and collaboratively with me in 2003 and 2004. Tape-recorded territorial playback calls were also used to localize flicker

territories and subsequently nest sites. When clutches were complete, a small door was

cut into the side of the nest tree for access to adults, eggs, and nestlings (Wiebe 2001).

At the end of each field season, to avoid excessive disturbance to the nesting pair,

characteristics of the nest site and surrounding habitat were measured (see Chapter 2).

Each nest was checked on average every 4.2 days with a ladder, flashlight, and mirror to

monitor nest contents. Nest fate was determined following the criteria in Wiebe (2003).

1.5 Trapping and Banding Adults

After adults were captured by flushing them from the cavity into a net placed

over the cavity entrance, each was fitted with a combination of four leg-bands (two per

leg) for individual identification. I also sexed and measured lengths of the wing, bill,

tail, tarsus, 9th primary, and weighed each captured flicker. For a multivariate index of

body size (Rising and Somers 1989), I used the score on the first axis of a Principal

Component Analysis (PCA1) based on measures of: lengths of the wing, bill, tail, tarsus,

9th primary, and bill depth. Separate PCA analyses were done for each sex because of

sexual size dimorphism (Wiebe 2000). For an index of nutrient reserves, "body

condition", I used the residuals of a Reduced Major Axis (RMA) regression of PCA1

and body mass (Green 2001). Age was assessed using either plumage characteristics

(Moore 1995) or from banding records of recaptured birds.

CHAPTER 2
NEST SITE ATTRIBUTES AND TEMPORAL PATTERNS OF NEST LOSS OF
NORTHERN FLICKERS: EFFECTS OF NEST PREDATION AND COMPETITION

2.1 Introduction

Nest predation accounts for an average of 80% of nest failures across a wide

range of species, habitats, and geographic locations (Martin 1993). Nest predation

typically results in the loss of the entire clutch, reducing parental fitness (Li and Martin

1991). Predation risk has both a spatial and temporal component leading to observable

patterns throughout the landscape and over time (Willson et al. 2003). Many studies

have examined predation on bird nests, but most have examined only nest site selection

in response to one nest predator or have not considered responses to different predators.

Birds contend with a rich guild of nest predators, each with differing search strategies

and differing affinities for prey types that potentially lead to trade-offs in nest selection

to avoid different predators (Sih et al. 1998). Furthermore, competition for nest sites,

where offspring are killed, result in reproductive loss similar to predation, but this has

rarely been examined in conjunction with loss to predators. Here I document nest

selection and temporal aspects of Northern Flicker nesting in relation to nest loss to

mammals and an avian competitor, the European Starling.

Cavity nesters may experience relatively low nest predation rates compared to

open-cup nesters (Martin and Li 1992), but nest predation still remains the largest source

of nest loss for cavity nesters and therefore has the potential to influence nest selection

(Nilsson 1986). However, one must interpret these generalizations with caution, as most studies of predation rates on cavity nesters have used nest boxes which may bias results by enhancing nest survival (Møller 1989). I overcame this potential pitfall by evaluating nest predation and nest competition in a population of Northern Flickers nesting in natural cavities.

Most studies to date have focused on the spatial aspect of selecting a safe nest site and have documented a hierarchy of selection from broad landscape-level traits to narrow microhabitat traits. Several hypotheses have been developed concerning how nest placement evolved as a result of predators developing search images for nests (Filliater et al. 1994). Nests that are easy to find and access should be depredated more frequently, resulting in selection for more concealed nests (concealment hypothesis: Cresswell 1997). To avoid ground-foraging predators, selection should favour higher nests (nest height hypothesis: Li and Martin 1991). For cavity-nesting species, the diameter of the nest entrance can limit the size of predator that is capable of entering the cavity; however, the diameter must be large enough for the resident to enter (Wesolowski 2002). High rates of nest predation along edges is common in forest landscapes, and so nests placed further from edges should experience reduced predation; however, evidence for this remains equivocal (Paton 1994; Lahti 2001; Bayne and Hobson 2002). If predators remember previous nest locations and consequently depredate them from year to year, those specific areas or nest sites should be avoided (Sonerud 1985a; Pelech 1999). If predators encounter a high density of nests it may lead to either development of a search image or increased search effort, and result in higher predation risk for nests in high density clusters compared to nests in low density

clusters (Niemuth and Boyce 1995). In general, the risk of nest predation will depend on (1) variation in predator abundance or behaviour and (2) predator species richness (Filliater et al. 1994).

To determine whether competitors exert pressures on nest site selection we must determine those nest characteristics that are preferred by the nest competitor. European Starlings are an introduced cavity nest competitor in British Columbia (first reports of breeding starlings occurred in 1951; Peterson and Gauthier 1985), and it has been suggested that recent declines of cavity nester populations (e.g., Northern Flicker) are due to intense competition with starlings (Moore 1995). However, the role of starlings in the declines of native cavity nesters may be overrated (Koenig 2003).

Temporal patterns of nest predation have not been examined as widely as spatial patterns because analytical techniques were lacking. The recent introduction of the nest survival analysis component of program MARK has made temporal analysis of nest survival easier (Dinsmore et al. 2002) and has removed the problem of assuming constant daily nest survival throughout the breeding season (Mayfield 1961). Such analyses suggest that temporal peaks of predation during the breeding season do occur in such species as plovers (*Charadrius montanus*; Dinsmore et al. 2002) and ptarmigan (*Lagopus lagopus*; K. Martin unpubl. data). Peak periods of predation may occur because predators develop a search image for prey items after a certain lag time (Nams 1997) or else switch food items throughout the season depending upon energetic requirements or food availability. I am unaware of any study to date that has examined temporal patterns of nest predation in a cavity-nesting species. Examining temporal

patterns of nest loss could help identify factors that select for the different timing of reproductive activities during the breeding season.

Plasticity of clutch initiation date may allow nesting birds to avoid temporal peaks of nest predation during the breeding season and nest when it should be safer (Wiebe 2003). Although changing clutch initiation date may be a way to temporally avoid one predator, if the new date corresponds with the peak activity of another predator, then nest loss may remain the same or even increase. In the case of flickers, delaying clutch initiation could outweigh any benefits (Wiebe 2003).

Observed predators in my study area include: red squirrels (12 predation attempts videotaped, two successful), long-tailed weasel (observed once), pine marten (observed once), and black bears (occurring 10 times in the past seven years; K.L. Wiebe unpubl. data). Other possible predators in the area include northern flying squirrel and deer mice (Walters and Miller 2001), but neither have been observed directly preying on eggs (K.L. Wiebe pers. comm.). Because red squirrels are a main nest predator on my study site, I predicted that predation risk would be highest at nests: (1) closer to the ground, (2) less concealed, (3) in suitable squirrel foraging habitat, such as areas with substantial coniferous forest (i.e., an increased probability of squirrels encountering a cavity nest), (4) with large clutches (i.e., increased olfactory cues, Petit et al. 1989), and (5) with a high density of active cavities surrounding them. In years with large squirrel populations, encounters by squirrels with flicker nests may also increase and therefore I predicted that as squirrel abundance increased so would predation on flicker nests. Furthermore, I predicted that flickers may experience within-year peaks in nest predation by squirrels as a result of changes in squirrel foraging tactics during

summer (i.e., a shift from arboreal to more ground-based foraging) and changes in squirrel food requirements (Pelech 1999). Changes in tactics of foraging squirrels could increase the number of encounters with flicker nests and thus increase predation risk on nests at certain times during the breeding season.

If starlings prefer certain nest sites, they may compete more intensely for flicker nests with those attributes (see Mazgajski 2003). Lastly, I also expected peaks of flicker evictions by starlings at the beginning of the flicker breeding season when starlings are prospecting for suitable nests and most takeovers usually occur (Wiebe 2003).

I examined whether a suite of flicker nest-site characteristics measured at five spatial scales were associated with one of three nest fates: successful, depredated by mammals, or evicted by starlings. I also used program MARK to model temporal trends of flicker nest loss spanning my seven-year dataset, considering predation and competition separately.

2.2 Materials and Methods

Nests were found following the procedure stated in Chapter 1 (see section 1.4, Locating and Measuring Nest Sites). I analyzed characteristics of nests with three possible fates. Successful nests fledged at least one young. I assumed a nest to be depredated when eggshell fragments were left inside the nest cavity and assumed, based on videotape evidence, that squirrels were the main nest predator. Whereas mammals tend to leave eggshell fragments in the cavity, starlings remove flicker eggs and deposit them outside the nest (Wiebe 2003). A nest was considered lost to starlings when the following sequence of events occurred: (1) flickers began laying and were observed in the nest cavity, and (2) I found a breeding starling in the nest cavity on a subsequent

visit and starling nesting material (green vegetation, which is a unique nesting characteristic of this cavity nester) was inside the cavity.

2.2.1 Nest and Site Characteristics

Pribil and Picman (1997) suggested that using only one spatial scale of habitat measurements was unreliable because it may omit habitat scales that are important for birds selecting nest sites. I measured nest characteristics, that were important predictors of nest predation on cavity nests in other studies (Nilsson 1984; Rendell and Robertson 1989; Christman and Dhondt 1997; Hooge et al. 1999) and were reflective of habitat preferences of squirrels (Bayne et al. 1997) and starlings (Mazgajski 2003), at five spatial scales: (1) cavity - cavity dimensions, (2) nest tree - measurements associated with the tree itself, (3) small nest tree plot - a 2-m radius surrounding the nest tree, (4) large nest tree plot - an 11.2-m radius (0.04 ha) surrounding the nest tree, and (5) landscape level - beyond 11.2 m up to several kilometers (Table 2.1). Data on number of squirrel detections per hectare per year on the Riske Creek study area using point counts following protocol presented in Martin and Eadie (1999) were obtained from K. Martin (unpubl. data). Four lines 500 m long each (20 ha) were placed on 11 plots, representing a range of forest types and fragmentation, on the Riske Creek study area (Martin and Eadie 1999). Point count stations were established 100 m apart and fixed radius (50 m) points counts were conducted for 6 min to detect, both visually and acoustically, bird species and cavity nesting mammals (Martin and Eadie 1999). The number of red squirrels detected was then standardized every year according to the total area covered by the point count lines (K. Martin unpubl. data).

Table 2.1 Characteristics of nest tree and surrounding habitat measured for all flicker nests between 1998 and 2004 at Riske Creek, British Columbia.

Scale	Characteristics Measured
Cavity	Cavity entrance width (cm)
	Vertical depth (cm)[b]
	% vegetation concealment within 1-m radius surrounding and perpendicular to the cavity entrance[c]
Tree	Cavity height from ground (m)
	Number of cavities, excluding the active flicker cavity
2-m radius surrounding nest tree	% vegetation ground cover[d]
11.2-m radius surrounding nest tree[a]	Number of aspen[e]
	Number of conifers[e]
	Number of cavities
	Number of used cavities (only in 2003 and 2004)[f]
Landscape	Distance to dry grassland edge (m)[g]
	Distance to wet edge (m)[h]
	Distance to continuous coniferous edge (m)[i]
	Clump area (ha)[j]
	% conifer content of the clump[k]

Table 2.1 (Continued)

[a] I used the British Columbia Ministry of Forests Inventory Standard of 11.2-m radius plots surrounding each nest tree (Aitken et al. 2002) as an index of tree species composition and habitat complexity of the area in which the nest was placed.

[b] Cavity depth was measured from the bottom of the entrance to the cavity bottom.

[c] Determined by dividing the 1-m radius plot into eight equal sections and visually estimating vegetation concealment within each area to produce an estimate of concealment for the complete circle. I assumed that concealment within a 1-m radius affected visibility of the cavity entrance from both above and below the cavity.

[d] At the 2-m radius plot, only vegetation >30 cm tall (above maximum shoulder height of the majority of small mammalian predators when in a foraging position) was included in the estimates of concealment. I followed the same protocol for determining concealment within this 2-m radius as I did within the 1-m radius of the cavity.

[e] Trees were counted only if their diameter at breast height was $\geq$ 12.5 cm (British Columbia Ministry of Forests Inventory Standard).

[f] 12-min observations (double the time used in other point-count protocol for cavity nesters; Martin and Eadie 1999) were made at each nest during peak cavity nester breeding times (May to July; Martin et al. 2004) in order to determine the number of cavity-nesting species nesting within an 11.2-m radius of flicker nests. A cavity nester was included only if it was observed entering a cavity; however, I did not check cavities for eggs. Observations were done on a subset of nest sites that were not covered by point count and nest searching areas in the nest web project by K. Martin (Martin and Eadie 1999). I assumed that data on detection of cavity nest sites by the nest web personnel were as reliable as my observations.

[g] I measured the distance to dry grassland or road edge using a measuring tape.

[h] I measured the distance to a stream or lake using a Global Positioning System (GPS).

[i] I measured the distance to a continuous coniferous forest edge using a GPS.

[j] Estimated by pacing two distances covering the length and width of the clump and then assuming an ovoid area. For nests within large or continuous forest tracts where it was not feasible to pace distances, I used digital air photos of the study area taken in 2000 and rendered in ArcView (v. 3.2, 1999) with nest points overlaid to calculate an exact estimate of clump area.

[k] A visual survey of relative tree species abundance was done to estimate percentage conifer content within a forest clump.

2.2.2 Nest Comparison Analysis

I first determined whether my index of squirrel abundance (detections of squirrels per hectare per year) on the Riske Creek study area was correlated with the percentage of flicker nest sites that were depredated. Secondly, I determined whether squirrel abundance was correlated with yearly estimates of daily nest survival calculated from the program MARK analysis below.

Two separate analyses of successful versus depredated (hereafter predation analysis) and evicted nest sites (hereafter eviction analysis) were completed. The data set from 1998 to 2004 was used with totals of 497 successful nests, 128 depredated nests, and 37 failures due to eviction by starlings (Fig. 2.1). If a cavity was used more than once in the seven-year period, one nest attempt was selected at random to be included in the analysis in order to avoid pseudoreplication. Where possible, nests that were lost to starlings were left in the analysis to maximize the sample size available for comparison with successful nests. However, when starlings usurped the same cavity multiple times I only included one observation in the analysis to avoid pseudoreplication. I considered each new nest chosen by the same individual over consecutive years as an independent unit of measurement as well as new cavities excavated in previously used trees. After removal of duplicated nests, the predation analysis included 227 successful and 81 depredated nests, and the eviction analysis included 213 successful and 18 nests lost to starlings.

Stepwise logistic regression was used in both analyses and included the following explanatory variables: cavity height, cavity entrance width, vertical depth of the cavity, number of cavities in the nest tree, percentage vegetation cover within a 1-m
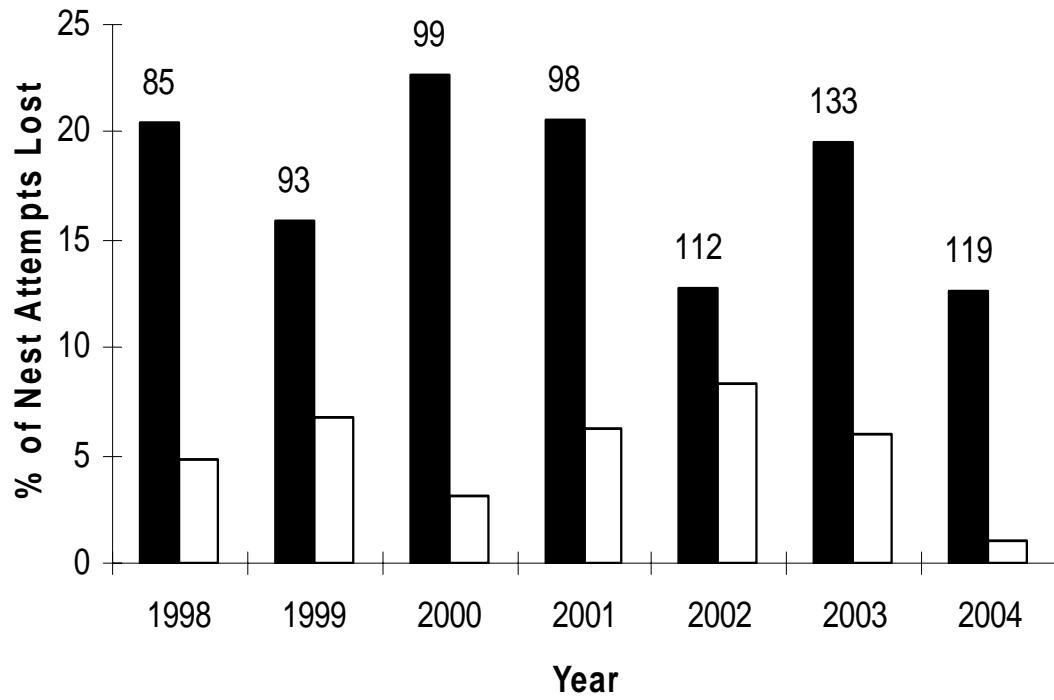
Figure 2.1 Total percentage of nests that were depredated (solid bars) or lost to starlings (open bars) at Riske Creek, British Columbia. Sample size of nests monitored each year is above the bars.

radius of the cavity entrance and 2-m radius of the nest tree, number of aspen, conifers

and cavities within an 11.2-m radius of the nest tree, distances to dry, coniferous forest,

and wet edges, the percentage conifer content of the active nest clump, and the size of

the forest clump containing the nest. I used a correlation analysis to reduce problems of

multicollinearity between explanatory variables. No pairs of variables exceeded the

usual multicollinearity standard of $r \geq 0.70$ (Compton et al. 2002) and the variables

included in the final model did not have inflated slope coefficients and standard errors

that would suggest multicollinearity (Hosmer and Lemeshow 2000). No variable met

the assumptions of a normal distribution (with the exception of cavity height) even after

transformations. The ratio of the number of cases to variables for the predation analysis

is approximately 19 to 1 and 18 to 1 for the eviction analysis, with a ratio of 20 to 1

being preferred for logistic regression analysis (minimum 10 to 1; Hosmer and

Lemeshow 2000). Five cavities had extremely large vertical depths (>90 cm) because

the whole core of the tree was decayed and hollow so these were removed as outliers

(standardized residuals > 3.0). I tested the classification performance and goodness of

fit (GOF) of each of the models using the area under the Receiver Operating

Characteristic (ROC) curve and Hosmer and Lemeshow GOF tests (Hosmer and

Lemeshow 2000). I only conducted surveys for other active cavity nesters within 11.2

m of flicker nests in 2003 and 2004; therefore, I analyzed this variable separately using a

non-parametric test.

2.2.3 Program MARK Nest Survival Analysis

      I analyzed daily probability of nest survival using two separate program MARK

analyses to evaluate temporal variation in nest loss, as well as effects of clutch initiation

date and clutch size (Dinsmore et al. 2002). Only 19 nests were lost in the nestling stage and therefore this analysis was confined only to the period between clutch initiation and hatching. The first analysis was set up so that each year was represented as a group in the encounter histories (i.e., seven groups representing nests from 1998-2004). In this case, nests that were defined as "lost" in the encounter histories included every type of nest loss (i.e., depredated, lost to starlings, lost to other species, nesting trees being blown over) except nests abandoned due to human disturbance (<2% of all nests lost). I also included three covariates in the models: clutch initiation date, clutch initiation date squared, and clutch size. I modeled linear and quadratic time trends of nest loss over the breeding season, as well as basic models of year differences and constant nest survival.

I conducted a second nest survival analysis to examine the temporal effects of two types of nest loss (predation and eviction). In this case, two groups were entered in the encounter history, such that one group was composed of all successful and all depredated nests, whereas the second was composed of all successful nests and nests lost to starlings. Inclusion of all successful nests in each group allowed for a controlled background of nests that survived to examine time trends of nest predation and nest eviction. I ran general models of group differences, linear and quadratic time trends, and basic models of constant nest survival.

Initially, quadratic time trend models would not reach numerical convergence. I corrected for this by specifying initial parameter estimates from the linear time trend models and then specifying varying initial values for the quadratic term until numerical convergence was reached (S. Wilson pers. comm.). I used AICc (AIC corrected for

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small sample sizes) to select the most parsimonious model in each analysis (Burnham

and Anderson 1998).

2.3 Results

2.3.1 Nest and Site Characteristics

Squirrel detections per hectare varied annually from 0.23 - 0.32. There was no

significant correlation between my index of yearly squirrel abundance and both the

percentage of nests depredated per year ($r = -0.13$, $N = 7$, $P = 0.78$) and year-specific

daily nest survival rates ($r = -0.04$, $N = 7$, $P = 0.93$).

A general description of flicker nest characteristics is presented in Table 2.2.

The predation analysis suggested that cavity height, vegetation within a 1-m radius of

the cavity and 2-m radius of the tree base, distance to coniferous edge, and the

percentage conifer content of the clump influenced the probability of a nest being

depredated (Table 2.3; Figs. 2.2 and 2.3). This model provided acceptable

discrimination between successful and depredated nest sites and fit the data (Area under

ROC $= 0.739$, $P < 0.001$; Hosmer and Lemeshow GOF test $X^2 = 4.27$, $P = 0.83$).

Conversely, the eviction analysis revealed that nests placed further away from

coniferous edges and in clumps with a lower percentage conifer content had an

increased probability of eviction by starlings (Table 2.3; Fig. 2.3). This model also

provided acceptable discrimination between successful and evicted nest sites and fit the

data (Area under ROC $= 0.759$, $P < 0.001$; Hosmer and Lemeshow GOF test $X^2 = 8.45$,

$P = 0.39$). For each significant nest feature (Table 2.2), I tested directly whether there

were differences in these nest characteristics between depredated and evicted nests using

non-parametric Mann-Whitney U tests. Similar to my logistic regression analysis, there

Table 2.2 Characteristics of 483 Northern Flicker nest sites at Riske Creek, British Columbia at five spatial scales. Each nest is included only once.

Scale	Variable	Mean	SD
Cavity	Height (m)	3.13	2.12
	Entrance width (cm)	6.4	0.9
	Vertical depth (cm)	39.6	12.5
Nest tree	Number of cavities	1	1
	% vegetation cover 1 m	4	10
Small plot	% vegetation cover 2 m	22	23
Large plot	Number of aspen	7	6
	Number of conifers	3	5
	Number cavities	1	2
Landscape	Distance to dry grassland edge (m)	11.2	13.9
	Distance to wet edge (m)	180	276
	Distance to continuous coniferous forest edge (m)	253	202
	Clump size (ha)	13.8	103.4
	% conifer content of forest clump	31	33

Table 2.3 Significant predictors of nest failure in separate logistic regression analyses on depredated nests and nests lost to eviction by starlings.

Analysis	Variable	B	SE	Wald	P
Predation					
	Height (m)	-0.406	0.130	9.78	0.002
	% vegetation cover 1 m radius	-0.098	0.034	8.22	0.004
	% vegetation cover 2 m radius	-0.021	0.009	6.05	0.014
	Distance to coniferous edge (m)	-0.003	0.001	8.12	0.004
	% conifer content of forest clump	0.009	0.004	4.01	0.045
Eviction					
	Distance to coniferous edge (m)	0.002	0.001	3.47	0.063
	% Conifer content in forest clump	-0.044	0.016	7.46	0.006
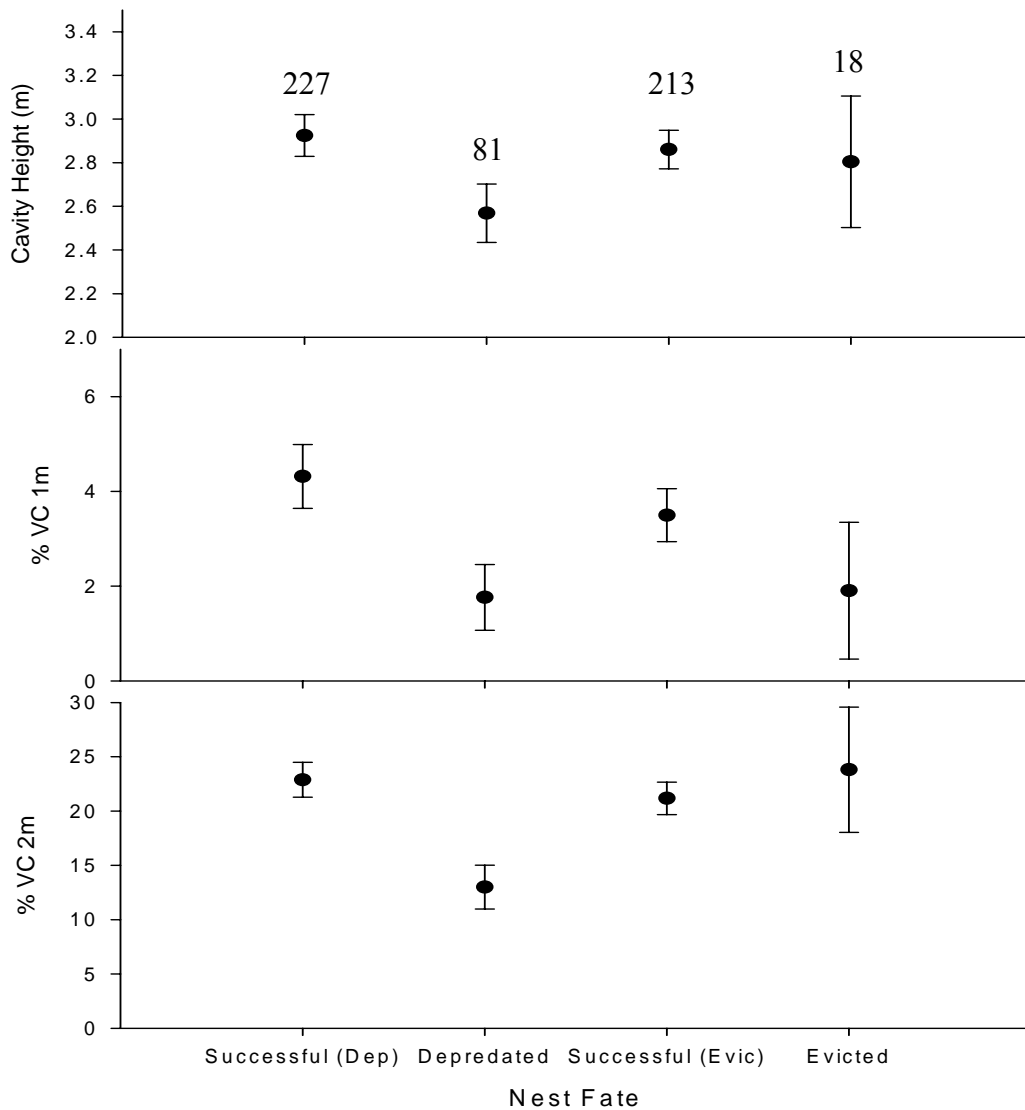
Figure 2.2 Means and standard error bars for three variables deemed significant by logistic regression analysis for predicting mammalian nest predation. For comparison, characteristics of nest sites usurped by starlings (and associated successful nests for each separate analysis) are also shown, although these three variables were not significant predictors of eviction. VC indicates vegetation cover within a 1-m radius of the cavity entrance or 2-m radius around the tree base. Sample size in each category is presented above each error bar.
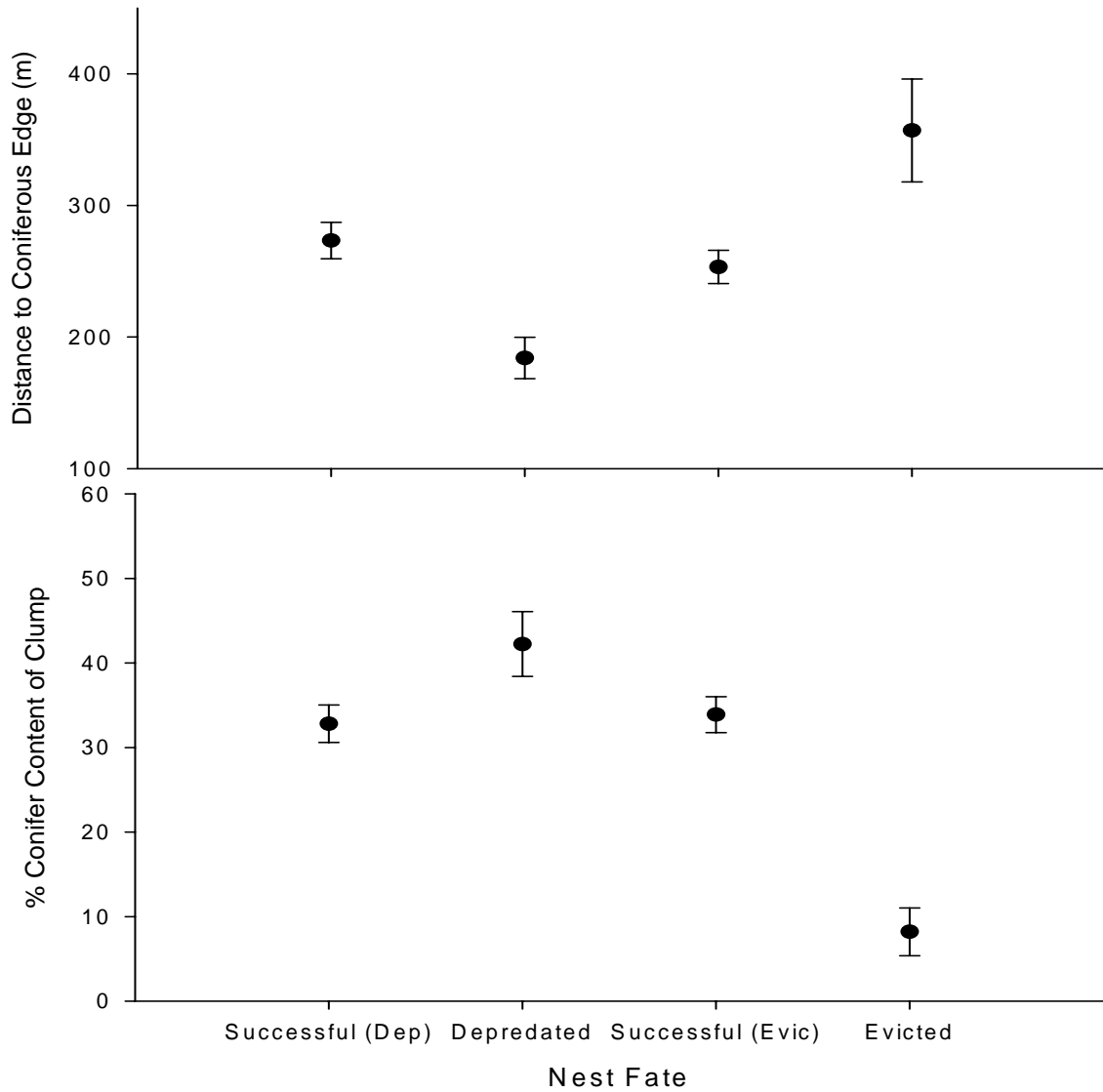
Figure 2.3 Means and standard errors of distance to coniferous edge and percentage conifer content of the nesting clump that significantly predicted both predation and eviction. Note that there are two means and error bars for successful nest sites corresponding to the random subsample of nests used in each separate comparison. Sample sizes in each category are the same as in Figure 2.2.

were no significant differences between depredated and evicted nest sites in nest height ($U = 816.5$, $P = 0.55$), percentage vegetation concealment within a 1-m radius of the nest cavity ($U = 892.0$, $P = 0.99$) and within a 2-m radius of the tree base ($U = 669$, $P = 0.07$). However, there were significant differences between depredated and evicted nests in distance to coniferous edge ($U = 416.5$, $P < 0.001$) and percentage conifer content of the forest clump ($U = 378.5$, $P < 0.001$). Nests that were usurped by starlings had approximately one more used cavity surrounding them than did either depredated or successful nests (Kruskal Wallis $X^2 = 13.87$, $df = 2$, $P = 0.001$), but this was based on a sample of only eight evicted nest sites.

2.3.2 Program MARK Nest Survival Analysis

The constant model (i.e., Mayfield daily nest survival) estimated daily nest survival probability during the egg stage (laying and incubation combined) at 0.985 (95% CI: $0.981 - 0.987$). The model with the highest AICc weight and lowest AICc value included a quadratic time trend (T+TT) plus effects of clutch size (CS) and clutch initiation date (CID) as covariates (Table 2.4, Fig. 2.4). Daily nest survival rates increased with increasing clutch size ($\hat{\beta} = 0.351$, 95% CI: 0.169, 0.532), but decreased with later clutch initiation dates ($\hat{\beta} = -0.268$, 95% CI: -0.509, -0.028). The best overall model was ($\hat{\beta} \pm$ SE): Logit (daily nest survival estimate) = $(4.96 \pm 3.79) - (0.07 \pm 0.26$ T) $+ (0.002 \pm 0.004$ TT) $+ (0.35 \pm 0.09$ CS) $- (0.27 \pm 0.12$ CID). There was little support for annual differences in daily nest survival (Table 2.4).

The second MARK analysis suggested that rates of predation and eviction on flicker clutches followed a quadratic time trend throughout the breeding season (Table

Table 2.4 All models analyzed using program MARK nest survival analysis with associated AICc values, ΔAICc, AIC weights (w_i), and the number of estimable parameters in each model (K). Models within 2 AIC units of the top model (ΔAICc =0) indicate some support of the observed data. Models with weights < 0.01 are not presented; however, the model of constant daily nest survival, S (.), is presented for comparison.

Model[a]	AICc[b]	ΔAICc[c]	w_i[d]	K
S (T+TT+CS-CID)	1018.95	0.00	0.67	5
S (T+TT+CS)	1021.01	2.07	0.24	3
S (T+CS-CID)	1024.24	5.29	0.05	4
S (CS)	1025.90	6.96	0.02	2
S (CS-CID)	1026.91	7.97	0.01	3
S (T+CS)	1026.98	8.03	0.01	3
S (.)	1042.47	23.52	0.00	1

[a] S indicates daily nest survival rate. Model factors include: year (year), constant daily survival (.), linear time trend (T), quadratic time trend (T+TT), clutch size (CS), clutch initiation date (CID).

[b] Akaike's Information Criterion with small sample size correction.

[c] Difference between individual models and the top model. Top model has ΔAIC_c=0.

[d] Estimates of the likelihood of the model given the observed data; all models sum to 1.00.
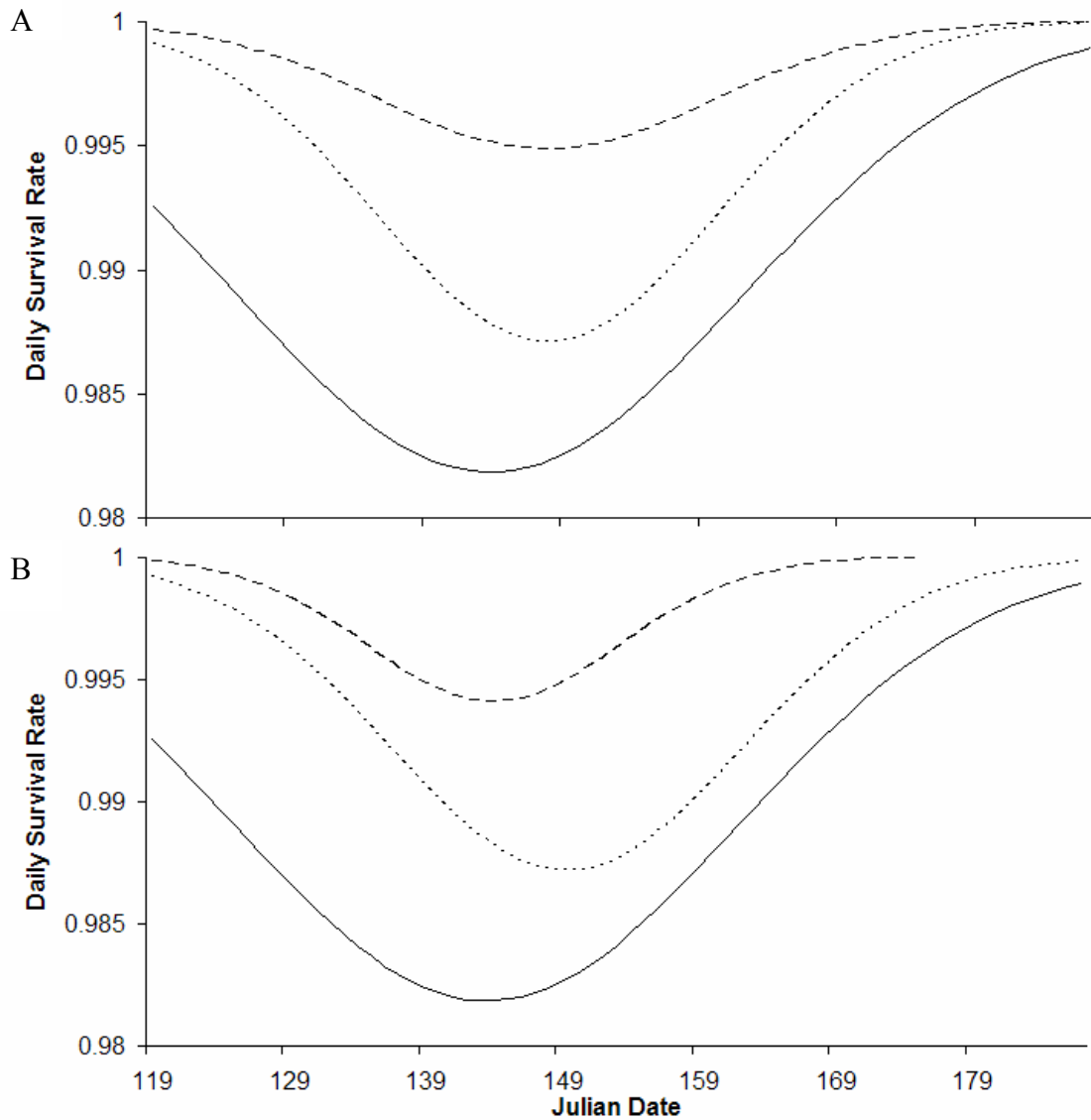
Figure 2.4 Timing of mammalian nest predation (····) and nest loss through evictions by European Starlings (---). The better model suggested that peaks of predation and eviction occur at the same time (A), however, the second more parsimonious model (Table 2.5) suggested that nest loss to eviction peaks five days earlier than nest loss to predation (B). The temporal pattern of all sources of nest loss (—) (Table 2.4) is included for comparison.

2.5; Fig. 2.4a); however, the second most parsimonious model suggested that peak eviction occurred five days earlier than peak predation (Table 2.5; Fig. 2.4b).

2.4 Discussion

2.4.1 Nest and Site Characteristics

Squirrel abundance was not correlated with flicker nest predation. My estimates of squirrels detected per hectare per year at Riske Creek were lower than other studies using constant effort squirrel trapping where squirrel numbers ranged from 1.5 - 2.8 per hectare per year (Krebs et al. 2001). As the range of squirrel detections per hectare per year on my study area was only approximately 0.1 compared with those other studies, it is possible that the magnitude of changes in squirrel abundance were not large enough to significantly affect nest predation rates. Because of a low sample size and only seven years of data it is also possible that I could not detect a correlation between squirrel abundance and nest predation.

Several cavity and tree characteristics were significant predictors of whether a nest would be depredated (Table 2.3). Despite a mean difference of only 0.5 m between successful and depredated nests, higher nests were more successful (Fig. 2.2). My estimate of the height of successful nests may be biased low if extremely high nests that I could not monitor (>8 m) were successful. However, I monitored more than 98% of nests. This is consistent with other studies that have found a height advantage in nest survival, particularly for open-cup nesters (Martin 1992), but higher cavities are not always safer (no effect of cavity height: *Melanerpes formicivorus* (Hooge et al. 1999), *Parus carolinensis* (Christman and Dhondt 1997), *Parus palustris* (Wesolowski 2002),

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Table 2.5 Models comparing timing of mammalian nest predation and nest eviction due to European Starlings. Table headings are the same as Table 2.4. Four models with weights <0.01 are not presented.

Model[a]	AICc	ΔAICc	w_i	K
S (g+T+TT)	983.47	0.00	0.54	4
S (g+T+TT+g*TT)	983.77	0.30	0.46	6

[a] Model factors included group differences between mammalian predation and nest loss to starlings (g) and a quadratic time trend (T+TT).

artificial nests (Purcell and Verner 1999), *Sialia currucoides* and *Tachycineta bicolor* (Holt and Martin 1997); positive effect of cavity height: *Troglodytes troglodytes* (De Santo et al. 2003), *Tachycineta bicolor* (Rendell and Robertson 1989), *Sturnus vulgaris*, *Parus caeruleus*, and *Parus palustris* (Nilsson 1984), *Bucephala islandica* (in nest boxes and natural cavities; Evans et al. 2002). Over the summer, squirrels may switch from arboreal feeding strategies to foraging on the ground (Pelech 1999) and therefore a small height advantage may deter a small arboreal predator climbing from the ground. A high nest cavity may also allow parents more time to dislodge a potential predator (Gutzwiller and Anderson 1987). Although high cavities may be safer, cavity height may be constrained because flickers require cavities with an adequate volume (Wiebe and Swift 2001), which is limited by the diameter of the tree trunk in higher cavities. My finding that increased concealment of the nest by vegetation can reduce nest predation either through camouflage of the nest itself or by increasing or encumbering predator search effort is also consistent with other studies (Martin 1992; Cresswell 1997).

At the mid-sized plot, nests that were lost to starlings had significantly more active nests surrounding them than either successful or depredated nests. Similar to brood parasitic Brown-headed Cowbirds (*Molothrus ater*) that apparently use host activity to find nests (Banks and Martin 2001), starlings may concentrate their search for nests in areas of high activity. However, these particular aspen groves may simply have common characteristics attractive to all cavity nesters in the nest web and be "hotspots" on the landscape (Aitken et al. 2002).

I suggest that the landscape-level variables (distance to coniferous edge and percentage conifer content of the clump) are associated with habitats where squirrels are most active. Squirrels on my study site forage preferentially and maintain middens in forest stands dominated by coniferous trees, followed by mixed stands, and lastly by deciduous-dominated tree clumps (K.E.H. Aitken unpubl. data), similar to other published studies outside my study area (e.g., Bayne et al. 1997). However, I could not ascertain whether my estimates of coniferous tree content in clumps were correlated with squirrel presence or absence. Squirrel activity should be higher in coniferous stands compared to deciduous stands so that nests in the former should be exposed to increased predation risk (Bayne et al. 1997). Conversely, starlings appeared to avoid stands dominated by conifers, which corresponds well with other studies that have found starlings nesting within 500 m of suitable foraging areas that are typically open grasslands (Feare 1984) and nesting in stands with high edge-to-interior ratios (Dobkin et al. 1995). At another study site near Riske Creek, Peterson and Gauthier (1985) found that starlings nested on the edge of forest patches, whereas flickers nested in sparsely treed groves. On my study area, Aitken and Martin (2004) found that starling nests were closer to grassland edges than random points. Starlings may also be avoiding predator habitat by nesting far from coniferous edges, but there is no evidence from other studies to support or refute this hypothesis.

Opposing pressures by multiple predators on prey behaviour have been well documented in aquatic systems, but less so in terrestrial systems (Templeton and Shriner 2004; see Sih et al. 1998 for a review). Crowder et al. (1997) suggested that interactions between predator types may complicate interpretations of observational data. For

example, survival of spots (*Leiostomus xanthurus*) was reduced in the presence of predatory flounders (*Paralichthys lethostigma*), but not in the presence of birds, nor in the presence of both predator types (Crowder et al. 1997). Controlled experiments set up in a factorial design (no predators, one predator alone, the other predator alone, and both predators present) are needed to determine the effect of multiple predators on prey survival. The large scales at which opposing pressures on flicker nest choice are occurring (compared to other studies, e.g., Sih et al. 1998) may make such experiments logistically difficult. It may be possible to conduct this type of experiment using predator-specific exclusion devices on natural or artificial nests in order to examine relative effects on flicker nest survival of both predators and competitors.

2.4.2 Temporal Patterns of Nest Loss

Daily nest survival was characteristically high as is typical for a cavity-nesting species (i.e., > 0.95, see Willson and Gende (2000) for a list of daily Mayfield nest survival rates for some cavity nesters), and never dropped below 0.98 in any of the models I tested. The rate of nest loss peaked in mid May and there was some support (i.e., $\Delta AICc < 2$) for the model where starling evictions peaked about five days earlier than predation (Fig. 2.4b). The peak date of starling loss calculated by program MARK (24 May – day 144) was similar to peak dates of evictions found by Wiebe (2003). However, I may have underestimated the risk of eviction early in spring because I could not detect all early evictions when flickers were defending a cavity, but had not yet laid eggs. It is also possible that I underestimated predation losses at the beginning of the season before all active nests were found. This could lead to the pattern of high initial nest survival followed by the peaks of eviction or predation in the time period when I

found most evicted and depredated nests. By the time of peak nest loss to predators on day 149, 79% of nests had been initiated, with a mean clutch initiation date of 138 ($\pm$12 SD), consistent with the hypothesis that predators do not begin to actively search for nests until most of the population has laid eggs (Niemuth and Boyce 1995). Furthermore, squirrels may actively switch food sources throughout the flicker breeding season, feeding primarily on vegetative and reproductive buds in spring, switching to other food sources such as eggs and fungi in mid summer and then harvesting and caching cones in late summer (Pelech 1999), potentially creating the period of peak nest predation that I observed.

Delaying nesting to avoid competition by starlings may not increase reproductive success if delayed nests have a higher risk of being depredated. Given that predation currently causes more nest loss than eviction (Fig. 2.1), it may not be advantageous for flickers in my population to alter clutch initiation dates in response to this nest competitor. The overall decline in clutch size with laying date also favours early nesting (Wiebe 2003).

2.4.3 Effects of Clutch Size and Clutch Initiation Date

Because larger clutches are exposed to predation for longer periods of time and may attract attention from predators through olfactory, visual or acoustic cues, it is generally believed that nests with more eggs should experience higher nest predation than those with fewer (Julliard et al. 1997). Contrary to this idea, smaller flicker clutches were depredated more often. Because eggs are hidden in the cavity, larger clutches should not be more conspicuous to predators (at least during incubation) and

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therefore clutch size may not influence predation risk directly. As clutch size is positively associated with female age (K.L. Wiebe unpubl. data) higher investment in nest defence by more experienced birds may increase nest security.

Nests initiated later in the breeding season were more likely to fail (Table 2.3). In this population there is a strong negative correlation between clutch size and clutch initiation date (Wiebe 2003), and fledglings that hatched later may have lower reproductive value similar to other woodpeckers (Witkander et al. 2001). Perhaps nest abandonment or decreased parental care reduces nest survival late in the season regardless of nest predation or competition.

2.4.4 General Conclusions

To date, most studies of the success of bird nests have combined all sources of loss, although Rauter et al. (2002) is an exception. Similar to other nest predation studies, I documented some nest features that apparently decrease risk of predation by mammals with no trade-off with respect to security from starlings. However, I also documented opposing pressures on nest-site characteristics as a result of predation and competition, and found that these opposing pressures operate on a landscape, rather than microhabitat scale. There seems to be an abundance of cavities and snags on my study area (Aitken and Martin 2004), but in more managed landscapes, nest characteristics may be constrained by the location and types of suitable nest trees and the number of competitors. If nest sites for cavity nesters are limiting, then constraints on nest choice at the landscape scale may have greater consequences for reproductive success than constraints of cavity or snag type at the four smaller scales I described.

Clark and Shutler (1999) suggested that nest loss is unpredictable, so differences between successful and unsuccessful nests may be small and difficult to detect with short-term studies. Starlings are a relatively novel nest competitor for flickers on my study area compared to sciurid nest predators and destroy fewer nests, so patterns of nest selection in response to eviction may not be as strong as for predation. As starlings become more abundant in western North America, selection on the timing and placement of nests to avoid nest competition may increase. Whether or not long-term shifts in nest characteristics of flickers and other cavity nesters are observed may depend on the relative strength of opposing selection pressures.

CHAPTER 3
EFFECTS OF NEST PREDATION ON BREEDING DISPERSAL OF NORTHERN
FLICKERS

3.1 Introduction

Breeding dispersal is the movement by adult birds from one breeding site to

another. If dispersers have greater reproductive success than non-dispersers, then

dispersal should increase parental fitness (Greenwood and Harvey 1982). Proximate

causes of breeding dispersal have been classified into two categories: site quality (site

choice hypothesis of Greenwood and Harvey 1982) and mate quality (mate choice

hypothesis of Greenwood and Harvey 1982). If a change in nesting location is

accompanied by a change in mate, it is often difficult to separate the causal effects of

each (Harvey et al. 1979a). In this paper, I concentrate on breeding dispersal in the

context of past reproductive success.

After nest predation, within- and between-year breeding dispersal should be

advantageous if predation is spatially and temporally predictable (Greenwood and

Harvey 1982; Sonerud 1985a; Powell and Frasch 2000). Dispersal distance often

increases following poor reproductive success (Haas 1998; Hoover 2003; Shutler and

Clark 2003), but this is not always the case (Lindberg and Sedinger 1997; Blums et al.

2003). By moving to a new area, birds may forego local knowledge of food sources and

refuges from predators, but may gain safer nest sites and higher quality territories or

mates (Forero et al. 1999). At any spatial or temporal scale, dispersing should only be adaptive when fitness benefits outweigh costs; however, the costs and benefits of dispersing may be sex-specific. In monogamous species, the sex that invests relatively more into nest construction and territory defence may be less likely to disperse due to costs of finding, constructing, and defending a new nest site (Greenwood and Harvey 1982).

Within-year dispersal (i.e., renesting) may involve many of the same costs and benefits associated with between-year dispersal. In addition, factors such as increased probability of predation during a long-distance move (Forero et al. 1999), time and energy invested in constructing a new nest cavity (Barclay 1988), increased competition for nest sites (Aitken and Martin 2004), and finding a suitable nest site late in the season (Pinkowski 1977; Greenwood and Harvey 1982), could add to the cost of renesting. The timing of predation within a short breeding season may also influence the likelihood of dispersing, so that adults whose nests were depredated relatively late in the season may not have enough time to disperse (Jackson et al. 1989). As well, late-hatched fledglings may have lower recruitment than early-hatched individuals (Witkander et al. 2001).

Few studies have examined whether direct encounters with predators before eggs are laid influence the decision of whether to disperse to a new nest site (Sieving and Willson 1998). Direct cues of predation risk (visual, olfactory, acoustic) should provide precise information on future predation risk (Thorson et al. 1998; Orrock et al. 2004). Detecting a predator near the nest early in the breeding cycle may be sufficient motivation to move because little investment has been made in nest construction or reproduction and there is still adequate time to nest. In such cases, costs of moving may

be small, compared to the possibility of complete reproductive loss later in the season. Møller (1988) hypothesized that Blackbirds (*Turdus merula*) could use the presence of Black-billed Magpies (*Pica pica*; a blackbird nest predator) as a cue of a high probability of future nest predation risk and predicted that blackbirds would consequently choose nest sites far from magpies, but this was not the case.

Northern Flickers are primary excavators, experience variability in nest loss due to predation (about 18 % at Riske Creek; Chapter 2), and reuse cavities more than most woodpecker species. Studies on dispersal of cavity nesters usually rely upon nest boxes to facilitate recapture (e.g., Shutler and Clark 2003); however, several biases may be inherent in these studies, such as unnatural predation rates, dispersal to natural nest sites is often not monitored, and the distances between nests are human determined (Møller 1989). I tested whether male and female flickers breeding in natural cavities were more likely to disperse between and within years after their nest had been depredated, relative to successful individuals, and whether reproductive success was higher among individuals that had dispersed. I predicted that female flickers would disperse more frequently because they invest relatively little, compared to males, in nest construction and parental care (Wiebe 2004a). Female flickers take on average 13 days to renest (Wiebe 2005), suggesting that time constraints and potential fitness consequences (e.g., recruitment of late- versus early-hatched young) of nesting late are possible in this system. For renesting flicker pairs, I predicted that pairs losing their clutch late in the season would be less likely to disperse compared to pairs that lost a nest early in the season. I tested this prediction by comparing clutch initiation dates of the first nest of pairs that had moved from or remained at their original nest that was depredated. One

of the assumptions of the site quality hypothesis is that nest predation is spatially and temporally predictable. Because cavity nests are generally permanent, I could test this assumption by examining whether flicker nest sites were consistently depredated or successful from year to year, regardless of the pair nesting there. Lastly, I tested whether a direct encounter with a model predator before clutch initiation elicited nest abandonment.

3.2 Materials and Methods

3.2.1 Predictability of Nest Site and Forest Clump Safety

Regardless of the pair nesting at a given nest site or within an aspen grove (hereafter clump), these locations may be inherently safe or unsafe from nest predators (i.e., predictable). I used a chi-square analysis to compare whether nest fate in year t was associated with nest fate in year $t+1$ ($\alpha_{(2)}$=0.05). In Chapter 2, I found several landscape-level characteristics associated with higher risk of nest predation and therefore I examined whether clumps were predictably safe or unsafe between years. Although multiple snags may be available for renesting within a clump, landscape-level characteristics are likely similar for all such trees, compared to trees in different clumps. These forest clumps may contain predator territories and also constrain the movements of predators; for example, squirrels probably would not move between clumps because of the risk in crossing large distances in grassland habitat with little overhead cover (Pelech 1999). I randomly selected consecutive between-year nesting attempts within a clump (but at different nests within that clump) and tested, using a chi-square analysis, whether nest success within a clump in year t influenced nest success within the same

clump in year *t+1*. If there were multiple consecutive nesting attempts within a clump, one was randomly selected to be used in the analysis.

3.2.2 Influence of Male and Female Attributes on Nest Success

Because reproductive success may vary with age and familiarity with an area (Harvey et al. 1979b; Greenwood and Harvey 1982), I tested whether nest success was associated with flicker age or familiarity with the Riske Creek area before pooling age classes for the analyses involving between-year dispersal (section 3.2.3, Between-year Dispersal). I used one chi-square test to compare nest success among three age classes (1, 2, 3+) and another to compare nest success among birds in three categories that reflected familiarity with the study site: (1) 1-year-old recruits that had been banded as nestlings on the Riske Creek study site the year before (moderate familiarity), (2) newly banded individuals of any age (assumed low familiarity), and (3) individuals that had been captured and bred at least once before on the study site (high familiarity). I assumed newly banded individuals were the least familiar with the area; however, it is possible that these individuals were present on the site and were not banded in previous years. Every nesting attempt by each individual was included in this analysis.

3.2.3 Between-year Dispersal

Forty percent of banded flickers return annually to Riske Creek (Fisher and Wiebe in review) and therefore I monitored nest selection of these returning individuals. Dispersal of each sex was analyzed separately, as well as a subgroup of females whose males were not included in the male-only analysis. Females generally remained with the same male from year to year (Wiebe 2005), potentially duplicating results from the male

analysis if all females were pooled. The subgroup of returning "single" females

provided an independent measure of female dispersal in the absence of their previous

mates.

Separate chi-square analyses of males and females were used to assess whether a

successful or depredated nesting attempt in year *t* was associated with the frequency of

moving nests in year *t+1*. I also examined whether males and females switched or

stayed within the same nesting clump in year *t+1*, based on their nesting success in year

t. Furthermore, I used a test of two proportions to assess whether nest success differed

between birds that remained at their original nest or clump versus those that dispersed. I

assumed that each bird and each site change was independent (Wiklund 1996; Forero et

al. 1999). All statistical tests were two-tailed with α=0.05.

Finite or small study areas may bias dispersal estimates, because birds may

disperse farther than the limits of the study area (Clark et al. 2004). Within my study

area I am likely able to detect most dispersal events, because: (1) recapture efficiency of

flickers at the Riske Creek study area ranges between 0.80 and 0.90 (Fisher and Wiebe

in review), (2) average between-year dispersal distance of recaptured males is

approximately 63 m, which suggests that only birds at the periphery of my study area

disperse outside, and (3) there have been no band recoveries of individuals during the

breeding season outside of my study area. As stated earlier, only 40% of banded birds

are recaptured annually suggesting that dispersal outside of the study area is common

and goes undetected. Therefore I caution that my estimates of dispersal may be low.

3.2.4 Within-year Dispersal

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I monitored 37 renesting attempts during the summers of 1998 through 2004 by different colour-banded flicker pairs after depredation of their first nest. This was based on observations of individuals at the site of their second nesting attempt after their first attempt had been depredated. Only three females switched mates after nest loss to predation and therefore males and females were not analyzed separately, but rather as pairs. I also tested for differences in subsequent nest success among pairs that (1) stayed at the original cavity, (2) switched nest trees, (3) remained in the original clump or 4) switched clumps, using a Fisher's Exact test. Lastly, I tested whether there were differences in mean first clutch initiation date between pairs that changed nest sites after nest predation or remained at the original depredated nest.

3.2.5 Experimental Model Presentations

To test the hypothesis that birds use encounters with predators as cues of local nest predation risk when choosing a nest, I placed either a model predator (red squirrel; N=24) or control (Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*; N=24) at potential flicker nest sites. The blackbird model was chosen as a control because it is not a nest predator, yet it is common on the study area. When a flicker was observed excavating a new cavity or flushed repeatedly from a previously used cavity before a clutch was initiated, I randomly chose one of the models and fastened it 1 m from the cavity entrance with a bungee cord tied to the tree trunk. I then monitored parental behaviour for 5 min starting from when the bird was judged to be within the line of sight of the model. Because the perceived threat of the predator could vary with distance to the nest, I kept the model to cavity distance constant across trials. Flickers respond to models with slow, deliberate movements, unlike many other bird species (Wiebe 2004)

and therefore the 5-min time period should have been adequate to gain a representative sample of flicker behaviour. Territorial "chatter" calls of the squirrel or songs of the Yellow-headed Blackbird were played from the base of the nest tree during the trial to increase detectability of the model (Ghalambor and Martin 2002). I then checked nests three to five days after the trial to ascertain nest retention between the treatment groups; this delay avoided excessive disturbance by humans to the nesting pair. I used a Fisher's Exact test to determine whether control or predator groups had different frequencies of nest abandonment.

3.3 Results

3.3.1 Predictability of Nest Site and Forest Clump Safety

Regardless of the pair nesting at a particular site, nest success was not predictable from year to year (X^2 = 1.929, df = 1, N = 144, P = 0.17; Fig 3.1). Only 87 of 527 trees had consecutive successful nesting attempts, whereas only 11 trees had consecutive predation events. Furthermore, approximately 74% of depredated nests and 72% of successful nests in year *t* were not used the following year.

Similar to the results for nest sites, nest success within individual clumps was not predictable between years (X^2 = 1.88, df = 1, N = 91, P = 0.17; Fig 3.1); 80% of clumps that contained a successful nest in year *t*, had a successful nest in year *t+1*. However, clumps containing nest sites that were depredated in year *t* had a greater probability of being successful in year *t+1* than being depredated (Fig 3.1).

3.3.2 Influence of Male and Female Attributes on Nest Success
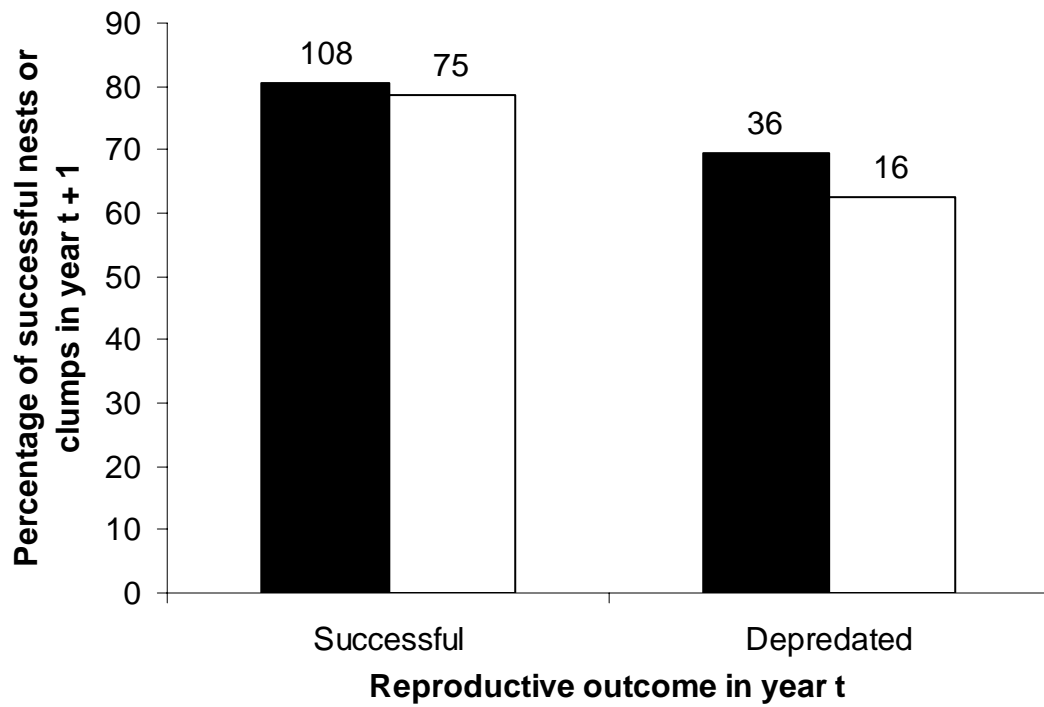
Figure 3.1 Percentage of successful nests (solid bars) or successful nests within individual clumps (open bars) in year *t+1* based on fate in year *t*. Sample sizes in each category are presented above the bars. Percentages are presented for comparison between reproductive outcomes, but numbers of nests or clumps that were successful or depredated were used in the analysis.

Neither male ($X^2 = 4.265$, df = 2, N = 568, P = 0.12) nor female ($X^2 = 4.385$, df = 2, N = 564, P = 0.11) age class influenced nest success (Fig 3.2a), nor did male ($X^2 = 1.961$, df = 2, N = 569, P = 0.38) or female ($X^2 = 4.302$, df = 2, N = 563, P = 0.12) familiarity with the study area (Fig 3.2b). Therefore, I was justified to pool all individuals of any age class or familiarity with the area for the following analyses.

3.3.3 Between-year Dispersal

The nesting outcome (successful or depredated) in year *t* did not have an effect on male or female dispersal frequency from nests in year *t+1* (males: Fisher Exact Test N = 159, P = 0.35, Fig. 3.3a; females: Fisher Exact test, N = 76, P = 0.99, Fig 3.3b). Approximately 73% of males and 96% of females switched nests after nesting successfully (Fig. 3.3). Sample sizes were small, but after predation there was no significant difference in the proportion of successful nests between male dispersers (six of eight attempts were successful) and non-dispersers (two out of five attempts were successful; test of two proportions, z = 1.26, P = 0.21, Fig 3.4a). I could not test whether female dispersers had greater reproductive success than non-dispersers because none stayed at their previously depredated nest (Fig 3.4a). Breeding success in year *t* did not have an effect on male or female dispersal frequency from clumps in year *t+1* (males: Fisher's Exact test, N = 159, P = 0.99, Fig. 3.3a; females: Fisher's Exact test, N = 76, P = 0.57, Fig. 3.3b). Individuals changing clumps after losing their clutch the previous year had the same proportion of successful nests as did individuals remaining within the original clump (Males: test of two proportions, z = 1.08, P = 0.28; untestable for females because none remained in the same clump after predation, Fig. 3.4b). All
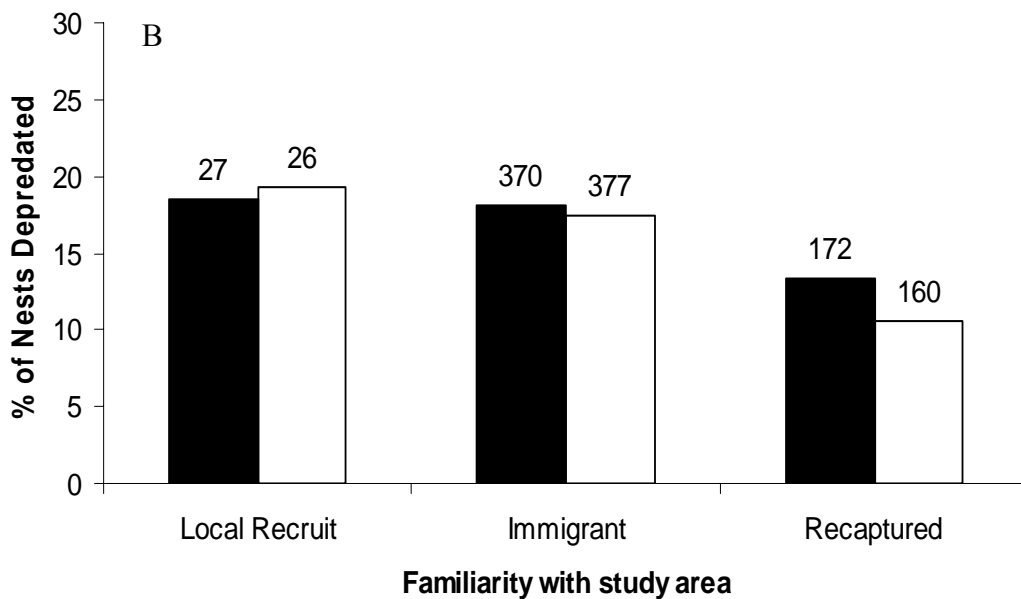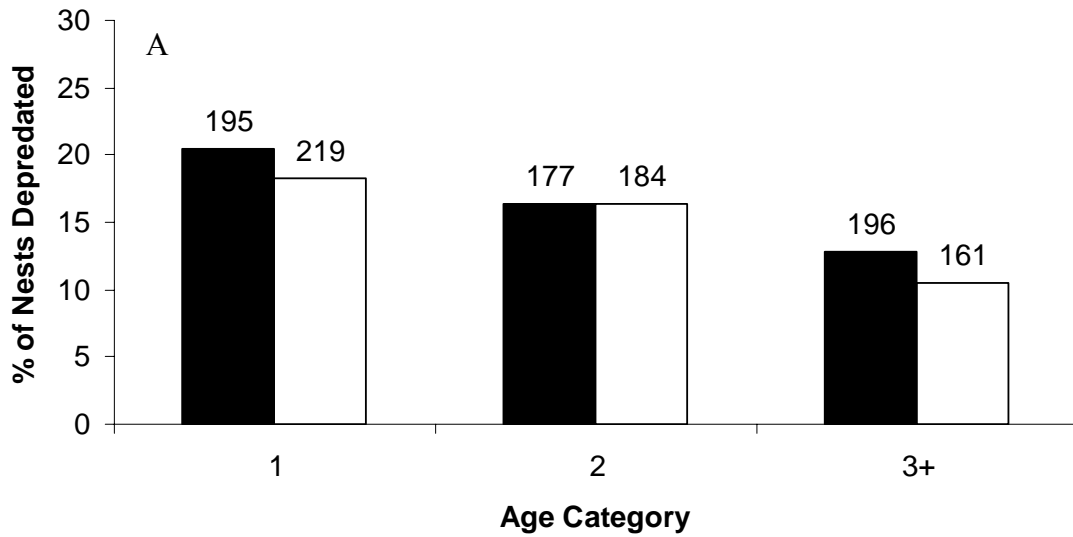
Figure 3.2 Influence of age class (A) and immigrant status (B; see text for description of each category) on the percentage of nests depredated for male (solid bars) and female (open bars) Northern Flickers at Riske Creek. Total number of nesting attempts by each age or immigration category is above each bar. Percentages are again presented for comparison purposes.
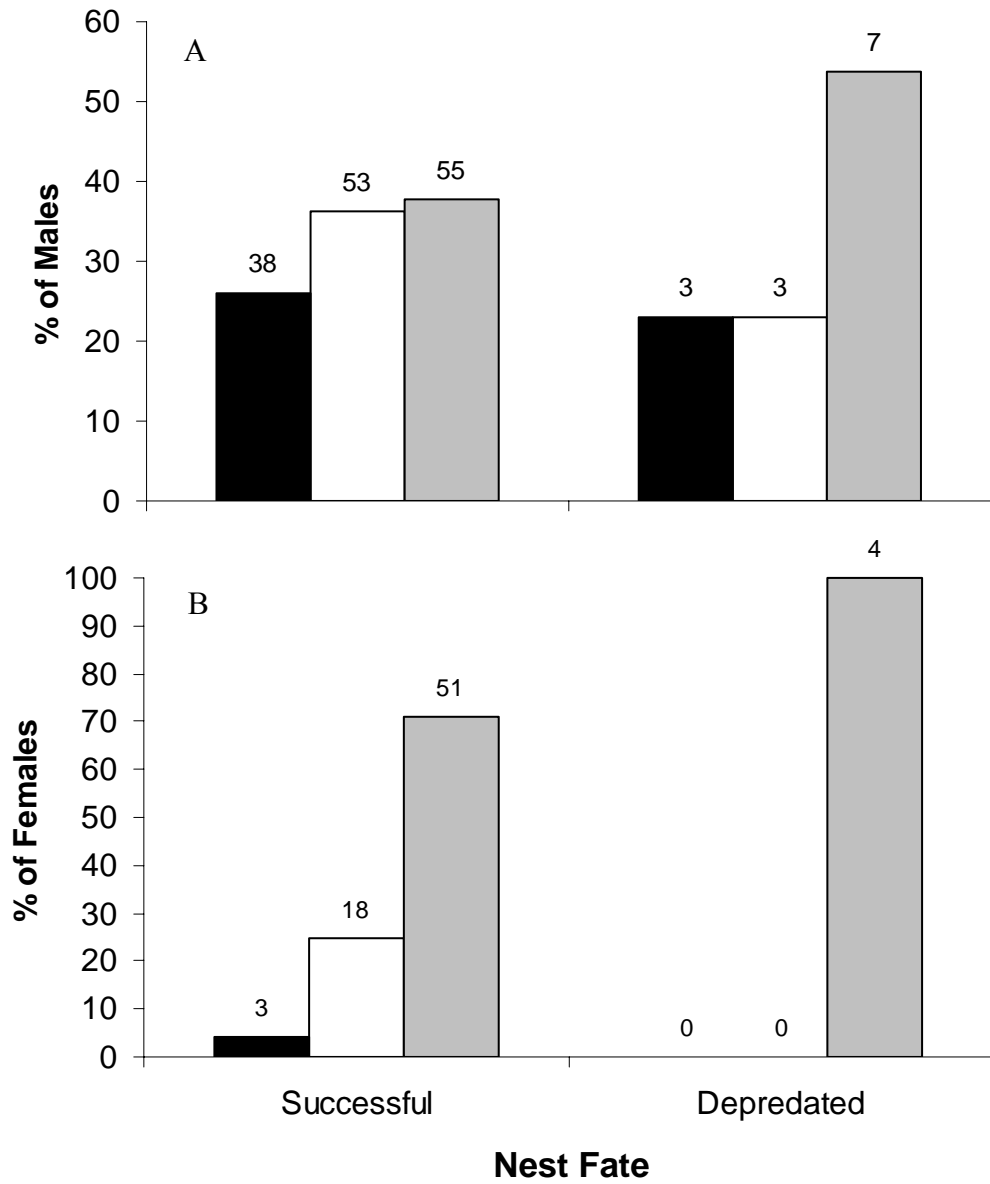
Figure 3.3 Between-year movement patterns of male (A) and female (B) flickers with respect to their nest fate the previous year. Black bars indicate the bird remained at the original nest, open bars indicate that the bird changed nests, but remained within the same forest clump, and grey bars indicate the bird changed nests and also changed clumps. Sample sizes are presented above the bars and percentages presented for comparison between groups.
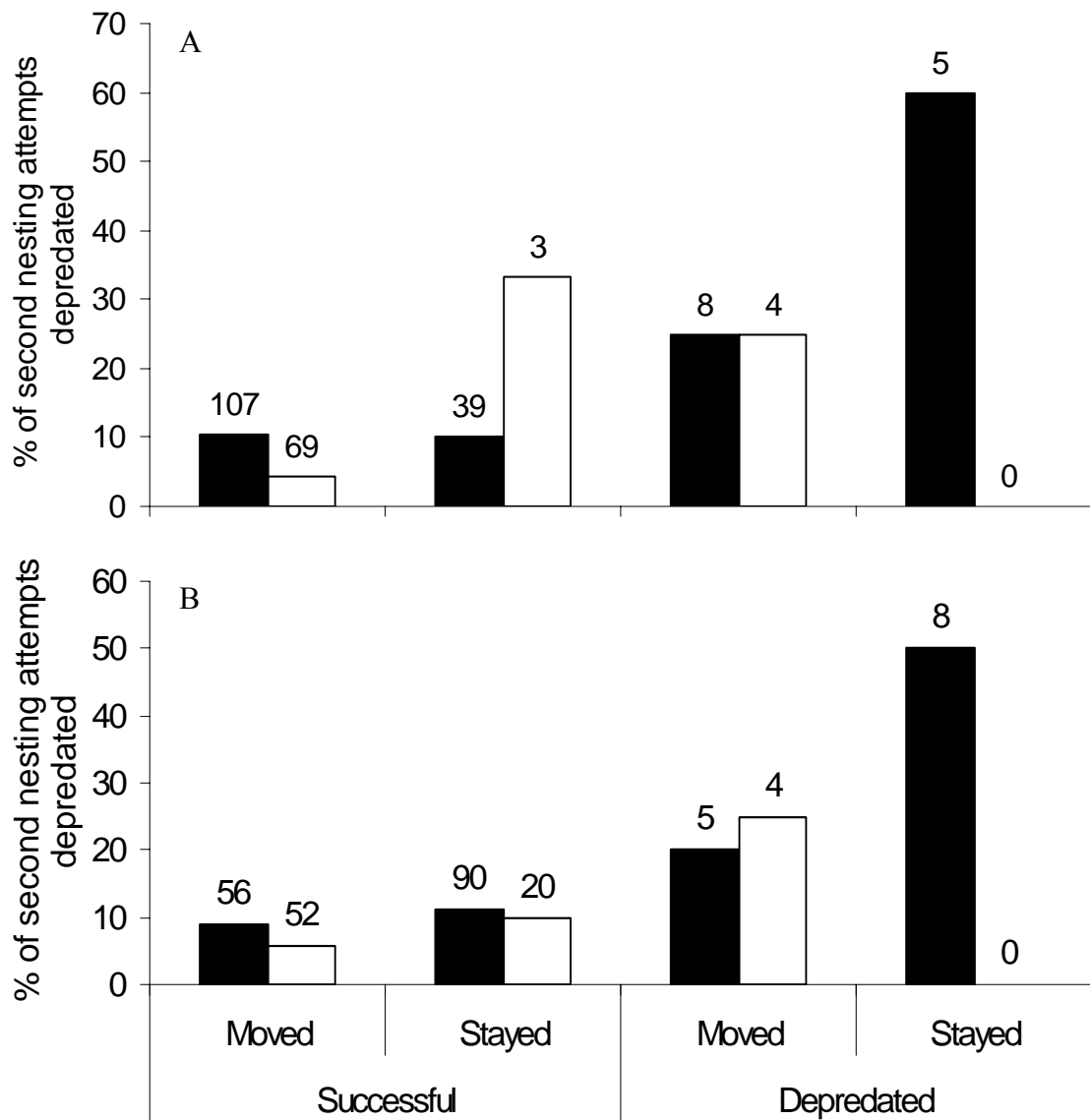
Figure 3.4 Percentage of individual males (solid bars) and females (open bars) that lost nests to predators after dispersing from (moved) or staying (stayed) at their original nest (A) or clump (B) in relation to past breeding success (successful, depredated). Total sample size of individuals is presented above each bar. Percentages are again presented for purposes of comparing between groups.

results for females using the full dataset (N=148) were consistent with results using the

reduced female dataset and therefore I only present results using the reduced dataset.

3.3.4 Within-year Dispersal

After nest failure, 27% of 37 renesting pairs used their original cavity, 32%

switched nests but stayed within the same clump, and 41% switched nests and clumps.

Of pairs that changed nest sites, an equal proportion stayed within the same clump

(N=12) as those that changed clumps (N=15; test of two proportions, z = 0.82, P =

0.41). There was an equal number of pairs that had successful nests after dispersing (21

out of 27 attempts were successful) compared with pairs that remained at the same nest

(8 out of 10 attempts were successful; Fisher's Exact test, P = 0.99). Dispersal beyond

the initial nesting clump had no effect on success of the subsequent nesting attempt

(Fisher's Exact test, P = 0.69).

3.3.5 Experimental Model Presentations

There was no significant difference in the frequency of abandonment between

pairs presented with either a control or predator model (3 out of 24 and 4 out of 24

abandoned nests respectively; Fisher's Exact Test, P = 0.99). Two of the three flickers

responding to the control model that abandoned their nests struck the model, whereas

such aggression to the control model was not observed in the other trials. I was unable

to examine whether or not energy investment into new cavity excavation played a role in

abandonment because sample sizes were low for pairs that abandoned a newly

excavated cavity (only two pairs abandoned nest sites that were newly excavated versus

five pairs that abandoned reused nest sites).

3.4 Discussion

3.4.1 Predictability of Nest and Clump Safety

In Chapter 2, I identified several nest-site characteristics that were associated with the probability of nest predation at both micro and macrohabitat scales. Predation risk at a nest site or within clumps was not predictable from one year to the next (Fig. 3.1). Although predation risk may be spatially predictable it may not be temporally predictable for several reasons (Carignan and Villard 2002). In particular, numbers of red squirrels are known to cycle and peak in mast years of cone crops (Krebs et al. 2001). Changes in predator density (increasing or decreasing encounters with prey items) or predator food preferences (i.e., squirrels focusing on cones in mast years and other food sources in years with less abundant cone crops) could influence the likelihood that squirrels encounter or attack nests, thereby influencing temporal patterns of predation. Models of nest survival incorporating yearly variation received more support than models with constant survival, which also points to temporally unpredictable nest predation (Chapter 2). K.L. Wiebe (unpubl. data) found that newly excavated cavities were no safer than reused cavities, suggesting that the lifespan or memory of predators is short and they do not consistently depredate known nests. Over many years, certain nests could show greater than average success compared to others if predation has a spatial component. By using only two consecutive years of nesting attempts, I was likely unable to detect "average nest success" for specific trees or within clumps even if temporal variation in nest predation was high. Another possibility is that individual (or pair) variation in vigilance or nest defence behaviour plays a larger role in the ultimate success of a nest than do nest characteristics (see Chapter 4).

3.4.2 Influence of Male and Female Attributes on Nest Success

Older birds generally fledge more offspring than younger birds because they acquire and retain safer nest sites or better territories (Payne and Payne 1993) and can effectively defend them against predators (see Chapter 4). Older pairs may also have higher nest success because they are more synchronized in sharing incubation and nest defence duties leaving the nest unattended less often than inexperienced pairs (K.L Wiebe pers. comm.). However, I found that neither male nor female age class affected nest success.

One of the costs of long-distance dispersal may be loss of familiarity with local resources and protective cover, such that immigrants may have lower reproductive success than individuals familiar with an area (Payne and Payne 1993). I found no evidence, however, to suggest that reproductive success differed between individuals with different levels of familiarity with the study area. Instead, first-time breeders in an area may use other cues to select optimal nest sites, such as the local reproductive success of conspecifics or interspecifics in a breeding patch (Doligez et al. 2002; Parejo et al. 2004). Using public information to select quality habitats, or relying on direct (visual, olfactory, acoustic) cues of predation, probably play a larger role than individual age or experience of flickers when selecting nest sites, perhaps because flickers are relatively short lived (K.L. Wiebe unpubl. data).

3.4.3 Between-year Dispersal

Reproductive success in year *t* did not influence whether males or females changed nest sites or clumps in year *t+1* and those individuals that dispersed from both nests and clumps did not produce more young. Predation is one of the most cited

proximate causes of breeding dispersal, but several studies have found no relationship

between nest predation and breeding dispersal (Dow and Fredga 1985; Korpimäki 1987;

Lindberg and Sedinger 1997; Shutler and Clark 2003; Blums et al. 2003). Other factors

such as mate switching or local food abundance may play a larger role in the decision to

disperse than does predation (Korpimäki 1987; Payne and Payne 1993). Increased

parasite loads in reused nests may be another motivation to disperse (Barclay 1988), but

I did not quantify nest parasite loads in this study.

If birds move to switch mates, dispersing birds should have new mates, whereas

non-dispersers should retain mates (Payne and Payne 1993). Wiebe (2003) found that if

both members of a pair returned, they stayed together about 75% of the time. As the

sample size of divorced parents is small, it is difficult to analyze whether mate switching

is related to dispersal. A fluctuating food supply may cause between-year dispersal,

such that dispersal distance should be negatively correlated with food supply

(Korpimäki 1987). Ants, which are the main food supply of flickers, are ephemeral and

fluctuate with temperature and rainfall (Elchuk and Wiebe 2003); therefore, it is

possible that the food supply of flickers may also fluctuate between years. Fluctuation

of the main food source of flickers may cause them to disperse in search of adequate

food resources regardless of predation risk and could also account for the tendency of

nests to be used intermittently, thereby allowing the local food supply to recover.

My estimates of between-year dispersal may have been low because dispersal of

flickers outside of my study area went undetected. Several studies have suggested that

small study sites may fail to detect dispersing individuals (Clark et al. 2004; Winkler et

al. 2004) and have found long-distance dispersal upwards of 25 km in small passerines

such as the Tree Swallow (Winkler et al. 2004). Clark et al. (2004) suggested that any hypotheses concerning avian dispersal must be addressed at larger spatial scales to overcome the problem of undetected dispersal.

3.4.4 Within-year Dispersal

Dispersal between nest trees or between clumps did not result in increased reproductive success as I had predicted if dispersal was an adaptive strategy to avoid local predators. Within-year dispersal has been less well-studied than between-year dispersal; however, within-year dispersal distance often increases after nest predation as was found in species such as Eastern Bluebirds, *Sialia sialis*, (Gowaty and Plissner 1997), Barn Swallows, *Hirundo rustica* (Shields 1984), Mallard, *Anas platyrhynchos*, and Gadwall, *A. strepera* (Ackerman et al. 2003), and Yellow-faced Honeyeaters, *Lichenostomus chrysops* (Boulton et al. 2003), but sometimes there is no significant relationship (Red-winged Blackbirds, *Agelaius phoeniceus*, Beletsky and Orians 1991). Significant decreases in dispersal distance after nest predation have even been observed in Hooded Warblers, *Wilsonia citrine* (Howlett and Stutchbury 1997). Perhaps immediate consequences of nest defence (i.e., unsuccessful nest defence action or injuries being sustained by the defending parents) have the potential to trigger dispersal even if it may not be a beneficial strategy (Powell and Frasch 2000). Although switching nests after predation was common, flickers did not move farther from their original nesting clump than movements within clumps, as I had predicted. As nest success was not different between individuals that moved or remained within the same clump, it is reasonable to assume that long-distance movements are not a particularly beneficial strategy to avoid predators.

I likely underestimated dispersal distances within the breeding season as some individuals disappeared after having their nest depredated. Techniques such as radio-tagging and tracking birds may have offered a definite location of where individuals had moved after nest predation (Powell and Frasch 2000). For example, of 128 nest predation events I was only able to track the renesting location of 37 pairs. It is possible that dispersing longer distances than within or between clumps (typically 50-300 m) may still be beneficial; however, I could not address this possibility.

Although it is common in many species that individuals disperse after having their nest depredated, less often have studies documented the reproductive consequences of dispersing. Surprisingly, dispersers did not produce more successful nests than non-dispersers, but this has been observed elsewhere (Clark and Shutler 1999). Finding a new cavity of high quality in a short time may be a challenge for cavity-nesting birds and other constraints such as competition and avoidance of nest parasites may be involved in the selection of renesting sites (Stanback and Dervan 2001). Eastern Bluebirds preferred to renest in successful nests only if those nests were parasite free (Stanback and Dervan 2001). For flickers, nest parasite loads may constrain the choice of locations for a renesting attempt, but thus far only qualitative data on parasite loads in flicker nests at Riske Creek have been collected. There was no difference in mean nest initiation dates between pairs that subsequently stayed or moved after nest predation, suggesting that seasonal time constraints on searching for a new nest were not a factor in short-distance movements within or between clumps. Peak times of nest predation occurred relatively early in the nesting period (29 May; Chapter 2) leaving approximately 30 days from that date until the latest nest initiation that has been

observed on the study area (K.L. Wiebe unpubl. data). Because the number of local recruits returning to the study area is less than 3% per year (Fisher and Wiebe in review) I was unable to test whether there are direct fitness costs of late-nesting, as is the case for other woodpeckers (Witkander et al. 2001). Whether or not longer distance movements are constrained by available time to renest and whether fledglings from later nests have lower recruitment than fledglings from earlier nests needs further investigation.

3.4.5 Experimental Model Presentations

Many studies have shown that birds may change foraging behaviour in response to olfactory, acoustic, and visual cues of predation (Kieffer 1991; Thorson et al. 1998; Orrock et al. 2004). I am unaware of any study to date that has experimentally tested whether encounters with predators may be incorporated into nest selection decisions by birds. Flicker pairs presented with a model predator did not abandon their nests more frequently than those presented with the control model. Some pairs may have perceived the Yellow-headed Blackbird model as a threat, because it may have resembled (at least to me) a European Starling; two of three pairs that abandoned their nest after encountering the control model attacked it. There are two possible interpretations that could account for the pair's unwillingness to abandon their nest when confronted with the model predator. Either birds did not perceive the predator model as a cue of future predation risk, or else did not perceive the model as dangerous, but in either case the benefits of moving did not outweigh any costs of remaining at the site where a predator was encountered. Flickers reacted in a similar way (diving, hitting, blocking the cavity) when responding to both real squirrels (R.J. Fisher pers. obs.) and to the model predator

(in this experiment and the following experiment examining nest defence, see Chapter 4) which suggests that the encounter was not a sufficient cue of future predation risk. For males especially, the costs of finding and excavating or renovating a cavity may outweigh the benefits of moving unless certainty of nest predation at the current site is high (Wiebe 2003). Competition for cavity nests is intense, frequently resulting in nest usurpation and loss of nest sites early in the breeding season (Aitken and Martin 2004), therefore, the cost of competing for a new nest may outweigh any benefit accrued from moving out of an area with an potential predator. As pairs that dispersed within the study site after natural nest predation did not have greater nest success, any benefits of moving locally after one encounter with a predator remain unclear.

Perhaps a single encounter with a predator is not sufficient to cause nest abandonment in cases where significant investment of time and energy has already been made into the current nest (Frid and Dill 2002). Continuous harassment by a predator may eventually cause nest abandonment and future studies could examine the effect of repeated model presentations to identify if there is a threshold of encounters that must be reached before nest abandonment takes place (Frid and Dill 2002).

CHAPTER 4
INVESTMENT IN NEST DEFENCE BY NORTHERN FLICKERS IN RELATION
TO AGE, SEX, BROOD SIZE, BODY SIZE, AND BODY CONDITION

4.1 Introduction

Parent birds may defend their clutch by selecting safe nest sites or by attacking

predators. Active nest defence may deter predators, but at the same time it may place

the parent bird at considerable risk and requires significant energy expenditure

(Blancher and Robertson 1982; Nealen and Breitwisch 1997; Olendorf and Robinson

2000). For example, defence elevates routine metabolic rates as much as 28% to 400%

in cichlids, *Neolamprologus pulcher* (Grantner and Taborsky 1998) and smallmouth

bass, *Micropterus dolomieu* (Hinch and Collins 1991; Steinhart et al. 2004). For many

bird species, the intensity of nest defence increases (1) over the breeding season with

increasing reproductive value of the brood (see Montgomerie and Weatherhead 1988 for

a review), (2) as the potential for renesting declines (Andersson et al. 1980), (3) with

clutch size or brood size (Olendorf and Robinson 2000), and (4) the intensity may

depend on the sex of the parent defending the nest (Breitwisch 1988; Sproat and

Ritchison 1993; Nealen and Breitwisch 1997).

Age may be correlated with the level of nest defence for several reasons, but this

has rarely been tested (Veen et al. 2000). It is likely that older birds have a reduced

probability of future reproduction and so they should place more value on the current

brood and invest relatively more compared to younger individuals (Hatch 1997).

However, age is often directly correlated with experience with predators and it is often difficult to separate the two because experienced and skilled individuals may also be willing to defend more strongly (Veen et al. 2000).

Costs and benefits dictate investment in nest defence by parent birds. Differences in levels of defence between the sexes have been the subject of many studies (e.g., Breitwisch 1988; Sproat and Ritchison 1993; Tryjanowski and Golawski 2004) perhaps because the comparison often is easy to test. Two of several important factors that may influence the level at which a given sex defends its nest are longevity and size dimorphism (Montgomerie and Weatherhead 1988). The sex with a lower survival rate and consequently a lower probability of breeding again should invest relatively more in their current brood compared to their partner (Montgomerie and Weatherhead 1988) and for many bird species the heavier investor is the female (Promislow et al. 1992). Sexual size dimorphism may also have an impact on levels of nest defence. Generally, the larger sex defends the nest more aggressively perhaps because the risk of injury is lower or it more effectively mounts a strong attack (Tryjanowski and Golawski 2004). Because healthy birds may have relatively lower energetic costs, they may take more risks when defending their nest than birds in poorer condition (Martin and Horn 1993). This may apply to sex-biased defence levels if, for example, females are in poorer condition after incubation and subsequently defend the nest less aggressively (Sproat and Ritchison 1993).

Cavity nesters may rely extensively on the inaccessible or cryptic nature of their nest (see Chapters 2 and 3) rather than nest defence (Weidinger 2002). Few studies have been conducted on defence responses of members of the family Picidae to nest

predators, but one has examined responses to the European Starling (Wiebe 2005). Anecdotally, De Kiriline Lawrence (1967) described woodpeckers "… taking up strategic positions inside the nest…" and employing "…vehement aggressive displays, vocalizations, and diving attacks". As well, De Kiriline Lawrence (1967) described a male Northern Flicker delivering a blow from its beak to a squirrel entering the nest hole, thus deterring the squirrel from entering the nest cavity.

In this study, I presented a model predator at nest sites of Northern Flickers to examine nest defence behaviour in relation to age class, sex, brood size, body size, and body condition of the defending adult. Because flickers are short-lived and apparently there are not age differences in survival (Fisher and Wiebe in review), I predicted that older birds would invest equally in nest defence compared with younger birds. Mark-recapture models suggested that male flickers have a 1-2 % lower apparent annual survival rate than females (Fisher and Wiebe in review). Therefore, differences in the probability of future reproduction between the sexes are likely small and thus I predicted that the sexes would not differ in their nest defence behaviour. Furthermore, male and female flickers invest relatively equal amounts of time into brooding and provisioning young (Wiebe and Elchuk 2003), which should also lead to equal investment in nest defence. If a large body size reduces the risk of any defence action then larger parents should defend more aggressively (Montgomerie and Weatherhead 1988). Conversely, if smaller parents are more maneuverable, then costs of defence may be low and smaller birds would be expected to defend more aggressively (Montgomerie and Weatherhead 1988). I also predicted that, within sexes, individuals in better condition would defend their nest with the highest intensity. Lastly, I predicted that individuals with large

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broods (high reproductive value) should defend their nest more aggressively than individuals with small broods (low reproductive value).

4.2 Materials and Methods

4.2.1 Model Presentations

The highest levels of nest defence generally occur during the nestling stage for species with altricial young (Montgomerie and Weatherhead 1988). I measured nest defence of flickers when nestlings were between 10 and 15 days old to control for effects of nest stage on defence behaviour. Each nest was tested once with a predator model (red squirrel) and once with a control model (Yellow-headed Blackbird or Cedar Waxwing, *Bombycilla cedrorum*) to avoid potential habituation of parents to the models (Knight and Temple 1986a; Knight and Temple 1986c). Furthermore, individuals were not repeatedly tested between years.

The protocol for model presentations was the same as in Chapter 3. In 2004, 27 control trials were conducted with a mounted Cedar Waxwing and its associated song, because the blackbird model suffered irreparable damage. Similar to the blackbird, waxwings are not a threat to flicker nests. Both predator and control models were placed at the nest site in random order with one to five days between presentations provided that nestlings were 10-15 days old. After models were placed at the nest, I retreated at least 15 m away to record responses of the returning parents.

Sex of the defending parent was determined by presence/absence of the moustache (present only in males) or identification of coloured leg bands. Ages of parents (up to four years old) were determined using molt criteria at the time of banding (Test 1945). Individuals were categorized as either one year old or adults (greater than

or equal to two years old) to increase sample sizes in each age category. An index of body size (PCA1) and condition (RMA) was calculated separately for males and females at the time of banding (see section 1.5, Trapping and Banding Adults). Brood size was measured at each nest after the second trial to avoid excessive disturbance to the nesting pair.

Behaviours of the adult(s) were monitored for 5 min after I had judged that the parent was within approximately 10 m and in line of sight of the model (see section 3.2.5, Experimental Model Presentations). I quantified flicker nest defence responses based on five behaviours recorded during this 5-min period: (1) response time of the adult (i.e., the time between when I had set the model up and was hidden, to when the parent returned and I judged it was within line of sight of the model), (2) number of alarm calls ("peah" and "wicka" calls; Moore 1995), (3) a visual estimate of the minimum distance approached to the model (m), (4) the number of dives and hits were condensed into one dichotomous variable (i.e., no dives or dives on the model) because there were only four cases where a bird dived at the model but did not hit it, and (5) number of seconds an individual spent inside the cavity during each trial (Cordero and Senar 1990). The time spent in the cavity should reflect investment in nest defence because being in the cavity prevents predation of the nest (Cordero and Senar 1990). Assessing the risk posed to the parent by blocking the cavity entrance is difficult. This defensive strategy may be safer than others because most of the parent's body is inside the cavity (Cordero and Senar 1990), but there are no avenues of escape for the parent. Lastly, parents sometimes returned together to defend the nest (23 out of 185 trials); therefore, I conducted two separate analyses on nest defence behaviours, one using only

individuals that returned alone and another using individuals that returned alone and as a pair.

4.2.2 Statistical Analyses

Response time was square-root transformed to meet assumptions of normality. I used non-parametric tests to analyze the number of alarm calls, the minimum approach distance, and time spent in the cavity because data transformations did not result in normality.

First, I analyzed each defence variable singly to determine which behaviours differed significantly between control and squirrel models, without any other effects. This avoided having to enter another variable (model type) in subsequent analyses involving age class, sex, brood size, body size, and body condition. I used appropriate paired tests for these analyses to account for both predator and control trials being at the same nest. This may have been more stringent than necessary because it was not necessarily the same individual that responded to each trial; however, independent tests produced consistent results with non-independent tests.

For those behaviours that differed significantly between model types, I subsequently analyzed effects of age class, sex, brood size, body size, and body condition on nest defence. As body size and condition are calculated according to sex these had to be analyzed separately for males and females. Some birds were not recaptured during the same year as the trial and thus an index of year-specific body condition was not available (I assumed body size remained unchanged from previous years), reducing sample sizes for analyses involving body condition. I used appropriate parametric or non-parametric tests to determine whether brood size was correlated with

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defence behaviour of males and females, in case costs and benefits of defending broods differed between the sexes (Dawson and Bortolotti 2003). A logistic regression was used to analyze the probability of diving at the predator including effects of age class, sex, and brood size. I also analyzed response time of adults to the predator model because it may provide an index of parental vigilance. Because I predicted that birds in poor condition may be less vigilant at the nest, I only tested whether body condition (and not body size) was correlated with response time to the predator. All tests were at $\alpha_{(2)}=0.05$.

4.3 Results

4.3.1 Model Differences

Ninety-one control trials and 94 predator trials were conducted in 2003 and 2004. Sample sizes of responding parents of both age classes and sex varied according to model type (Table 4.1). Analyses using only individuals returning alone and the full data set produced consistent results and therefore results using the full dataset are presented. There were no significant differences in the five defence variables between years or control model types (blackbird versus waxwing), so data from both years and both control types were pooled. Flickers dived significantly more at the predator model compared to the control model (28 predator trials versus 2 control trials; Fisher's Exact Test, $P < 0.001$). Flickers approached the predator model more closely than the control model (mean minimum distance to predator model $= 3 \pm 4(SD)$ m; mean minimum distance to control model $= 5 \pm 4(SD)$ m; Wilcoxon signed ranks test $Z = -4.98$, $P < 0.001$). Mean response time to each of the models was not significantly different (control response time $= 880 \pm 134(SD)$ seconds, predator response time $= 852 \pm$

Table 4.1 Sample sizes for nest defence trials. Totals presented include instances where both parents responded, plus instances where only one parent responded. Thus, sample sizes are larger than the total number of trials conducted for each model.

Model Type	Sex	Age	N
Control	Male	1 Year	11
		2+ Years	42
	Female	1 Year	19
		2+ Years	30
Predator	Male	1 Year	17
		2+ Years	43
	Female	1 Year	19
		2+ Years	25

188(SD) seconds; paired t-test, t = 0.40, P = 0.69). There was also no effect of model

type on the number of alarms calls (Wilcoxon signed ranks test, Z = -1.41, P = 0.16).

Parents spent more time in the cavity in response to the predator model compared to the

control model (Wilcoxon Signed Ranks Test, Z = -2.35, P < 0.001). Because of

significant differences between model types, whether the responding parent dived at the

model, the minimum distance approached, time spent in the cavity, and response time,

were included in the following analyses.

4.3.2 Effects of Parental Attributes and Brood Size on Nest Defence

There was no significant influence of an adult's sex, age class or their brood size

on the probability of diving at the predator model (Table 4.2). There was no significant

difference in mean body size or condition between males that dived at the predator

model or did not (body size: t-test, t = 0.13, N = 60, P = 0.90; body condition: t-test, t =

-0.80, N = 48, P = 0.43) and similar results were observed for females (body size: t-test,

t = 0.12, N = 44, P = 0.91; body condition: t-test, t = 0.14, N = 37, P = 0.89).

There were no differences between four sex and age classes (one year old males,

males at least two years old, one year old females, and females at least two years old) in

minimum distance approached to the predator model (Kruskal Wallis test, X^2 = 4.50, df

= 3, P = 0.21). Body condition, body size, and brood size were also not correlated with

minimum approach distances to the predator model by males (body size: Spearman rank

correlation, r_s = -0.18, N = 60, P = 0.18; body condition: Spearman rank correlation, r_s =

0.10, N = 48, P = 0.49; brood size: Spearman rank correlation, r_s = 0.14, N = 60, P =

0.27) or females (body size: Spearman rank correlation, r_s = -0.09, N = 44, P = 0.57;

body condition: Spearman rank correlation, r_s = -0.23, N = 37, P = 0.17; brood size:

Table 4.2 Results of a logistic regression on the probability of diving at the predator model including effects of sex, age class, and brood size. No variables significantly predicted the probability of diving at the predator model (N=104 flicker individuals).

Variable	B	SE	Wald	P
Sex	-0.14	2.67	0.01	0.96
Age Class	-0.50	0.83	0.36	0.55
Brood Size	0.02	0.31	0.01	0.95
Sex x Age Class	0.62	1.05	0.34	0.56
Sex x Brood Size	0.08	0.36	0.32	0.57

Spearman rank correlation, $r_s = -0.22$, N = 44, P = 0.15). Sex and age class were not associated with response times (Table 4.3) and body condition was not correlated with response time for males (Pearson r = -0.22, N = 48, P = 0.13) or females (Pearson r = -0.24, N = 37, P = 0.15). Brood size was also not correlated with response time for males (Pearson r = -0.13, N = 60, P = 0.32) or females (Pearson r = -0.18, N = 44, P = 0.25). Older males spent significantly more time in the cavity than one year old males, one year old females, and females at least two years old (Kruskal Wallis test, $X^2 = 9.93$, df = 3, P = 0.02; Fig. 4.1), but there were no significant correlations with body size, body condition or brood size (male body size: Spearman rank correlation, $r_s = -0.04$, N = 48, P = 0.79; body condition: Spearman rank correlation $r_s = -0.02$, N = 60, P = 0.92; brood size: Spearman rank correlation $r_s = -0.09$, N = 60, P = 0.51; female body size: Spearman rank correlation, $r_s = 0.03$, P = 0.87, N = 44; body condition: Spearman rank correlation, $r_s = 0.07$, N = 37, P = 0.68; brood size: Spearman rank correlation, $r_s = -0.06$, N = 44, P = 0.69).

4.4 Discussion

4.4.1 Sex Effects on Nest Defence

My results revealed no statistical differences between nest defence of males and females, confirming my initial predictions. Although many studies have found sex differences in nest defence by birds (Gill and Sealy 1996; Cawthorn et al. 1998; Pavel and Bureš 2001; Griggio et al. 2003) some have not, including studies on species such as the American Goldfinch, *Carduelis tristis* (Knight and Temple 1986b), and Red-backed Shrike, *Lanius collurio* (Tryjanowski and Golawski 2004). American Goldfinch

Table 4.3 Effects of sex and age class of flicker parents on their response time to a model nest predator. Results are from a 2-factor ANOVA (N=104 individuals).

Factor	Sum of Squares	df	F	P
Sex	39.91	1	5.54	0.26
Age Class	2.73	1	0.38	0.65
Sex x Age Class	7.20	1	0.03	0.86
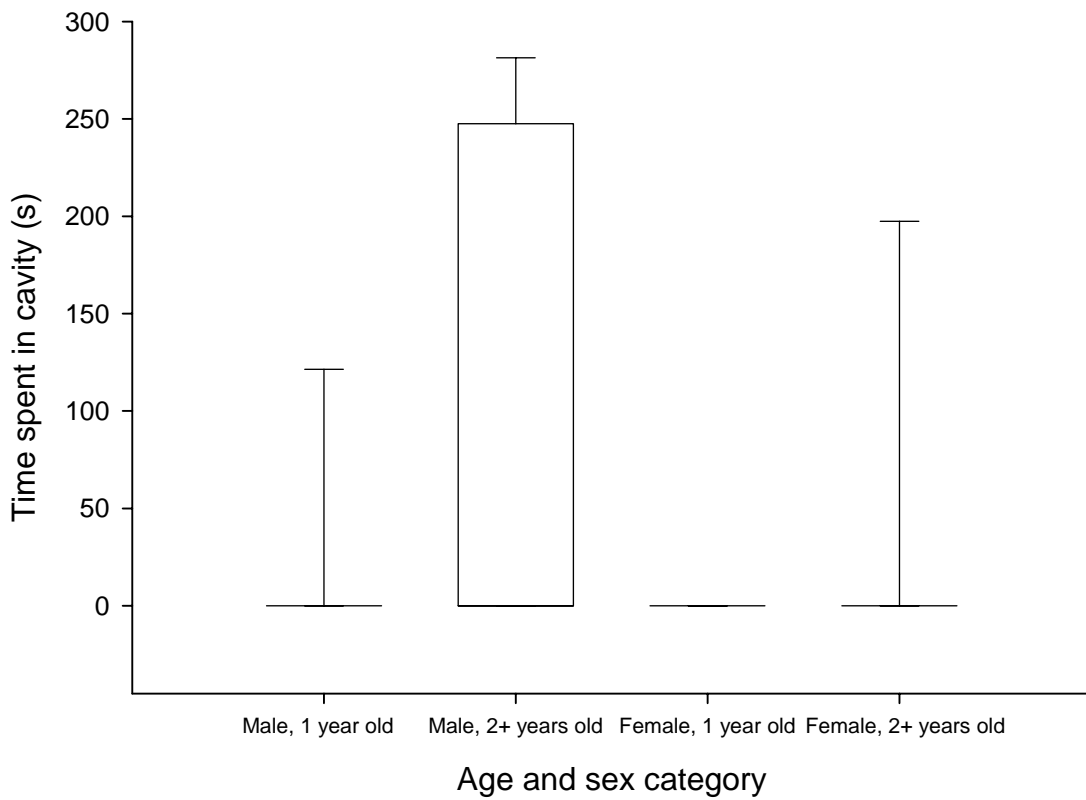
Figure 4.1 Time spent in the cavity by defending male and female flicker parents of different ages in response to a model predator. Horizontal lines indicate median values, boxes represent 75th percentiles and error bars are 90th percentiles. Sample sizes for each category are presented in Table 4.1.

are a monogamous species, with equal investment by the sexes into reproduction and therefore were expected to show equal levels of defence. Tryjanowski and Golawski (2004) suggested that because male Red-backed Shrikes were larger than females, but females had greater confidence of parenthood, differences in costs and benefits of nest defence between the sexes were nullified. For flickers, the sex differences in survival (males 1% lower than females; Fisher and Wiebe in review), body size (Wiebe 2000), and investment in the current brood (Wiebe and Elchuk 2003) are likely too small to alter the costs and benefits of defence between the sexes. Nest defence may be reinforced by interactions with nestlings, such that the sex with more contact with nestlings should defend the nest more intensely (Pavel and Bureš 2001). Flicker parents provision equally and although males spend 5% more time than females brooding and dividing food for nestlings (Wiebe and Elchuk 2003), this magnitude of difference does not appear to alter costs and benefits of nest defence between the sexes.

Males that were at least two years old spent significantly more time blocking the cavity entrance compared to younger males and females of any age. This particular behaviour can be used by cavity nesters to successfully prevent usurpation of cavities by more aggressive and dominant competitors (Cordero and Senar 1990). Cavity blocking was used by Tree Sparrows (*Passer montanus*) to prevent cavity usurpation by House Sparrows (*P. domesticus*) but not other competitors, suggesting that learning may be needed to develop this defence behaviour (Cordero and Senar 1990). My finding that older males blocked cavities more than younger parents may suggest a learned component of nest defence, but it is unclear why older females did not block cavities also. Blocking the cavity entrance with the head and beak in striking position may be an

effective strategy to minimize risk to the parent while still fending off an attack. It is difficult to directly quantify the "risk" of this defence behaviour and rank it with respect to the other behaviours I measured, but I assumed that diving at the model was probably riskiest. Perhaps birds perceive the risk of the various behaviours differently than I did. Nevertheless, there were few differences among the sexes for any behaviour, confirming the general conclusion that the sexes perceive overall costs and benefits of nest defence in a similar way.

4.4.2 Age Class Effects on Nest Defence

According to economic models of nest defence, older birds should defend their current brood more strongly than younger birds because they have lower future reproductive potential; however, there was no evidence for this in flickers. These results confirmed my original predictions and my previous finding that nest success of flickers was unrelated to age of the parents (Chapter 3). Winkler (1992) explained a lack of age effects in defence by Tree Swallows by the fact that these birds had age-independent survival. Annual apparent survival rates for flickers do not vary with age and they are a short-lived species (Fisher and Wiebe in review), so it was not surprising that age did not influence nest defence.

Although future survival is one component that could lead to age-dependent nest defence, experience may also play a key role (Montgomerie and Weatherhead 1988). Costs of nest defence are predicted to decrease with experience of the defending adult because strategies lessening the risk of defence may be learned over time (Montgomerie and Weatherhead 1988). It is difficult to control or test for effects of prior experience unless parents are experimentally exposed to predators multiple times. For this study, I

attempted to control for habituation to the models by only doing one model presentation per pair per year. This study design did not allow me to separate effects of parental age and experience.

4.4.3 Effects of Body Size and Condition on Nest Defence

It was surprising that neither body size nor condition influenced the five flicker nest defence behaviours that I measured. Because costs of defence should be lower for relatively larger birds (and birds in better condition), such individuals are expected to defend the nest more aggressively (Montgomerie and Weatherhead 1988). Although sexual size dimorphism is usually cited as important in creating differences in male and female nest defence (Tryjanowski and Golawski 2004), effects of body size within the sexes has rarely been tested (Hamer and Furness 1993; Radford and Blakey 2000). If there is an advantage to being smaller and more maneuverable when defending the nest, then costs and benefits for small birds may be comparable with larger birds (Montgomerie and Weatherhead 1988). Similarly, studies on effects of body condition within the sexes have been rare and produced results that are equivocal at best, ranging from no effect (Radford and Blakey 2000) to a sex specific effect (Winkler 1992; Hamer and Furness 1993). Evidence that body condition affects the intensity of active defence may be lacking, but good nutrient reserves may allow a parent to reduce foraging time away from the nest and be more attentive to the nest site during incubation and brooding (Slagsvold and Lifjeld 1989; Wiebe and Martin 1997) resulting in greater nesting success (Chastel et al. 1995). Flicker condition was measured in the late stages of incubation or early stages of brooding when parents could be captured and so may not be exactly representative of condition at the time of the defence trial. It is known that

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average body mass of adult flickers drops after nestlings hatch (K.L. Wiebe unpubl.

data), suggesting that my estimates of body condition may have been high. If relative

rankings of body condition among individuals remain similar until the mid-nestling

period, differences in nest defence still should have been apparent.

4.4.4 Effects of Brood Size on Nest Defence

I predicted that male and females flickers with larger broods should defend them

more aggressively, but brood size was not correlated with any of the defence behaviours

that I measured. It has been suggested that only brood size manipulation experiments

have the potential to adequately test for effects of brood size variation on nest defence

(Tryjanowski and Golawski 2004); however, experimental studies have also failed to

detect any differences in nest defence as a result of brood size (Tolonen and Korpimäki

1995). If parents have optimally adjusted their clutch size according to their ability to

raise all their young, then large and small broods may represent equal value to the

defending adults and therefore brood size may not influence nest defence (Tolonen and

Korpimäki 1995; Dawson and Bortolotti 2003).

4.4.5 General Conclusions

In conclusion, there were no strong relationships between level of nest defence

and age class, sex, brood size, body size, and body condition of flickers. This may be

explained by the relatively small differences in annual survival and size between the

sexes and by age-independent survival in this population. Older males spent more time

blocking the cavity entrance than any other sex or age class, but the costs and benefits to

the defending adult of this particular behaviour are unknown. I suggest that future

studies should examine other potential sources of variation in nest defence, such as nest

characteristics (e.g., nest height; Kleindorfer et al. 2005) and confidence of parenthood

(Montgomerie and Weatherhead 1988).

CHAPTER 5
SYNTHESIS AND RECOMMENDATIONS

5.1 Nest Sites, Breeding Dispersal, and Nest Defence

Mammalian predators more frequently depredated flicker nests that were closer to the ground, less concealed by vegetation around the entrance and at the base of the nest tree, closer to coniferous forest edges, and in forest clumps with a high percentage of conifer content. Proximity to coniferous edges or coniferous trees increased the probability of nest predation, but nests near conifers were less likely to be lost to starlings. Because red squirrels are the main predators of flicker nests and they inhabit conifer dominated forests, nest encounters by squirrels in these areas are likely higher. Flickers apparently face a trade-off in nest selection with respect to safety from predators or competitors. Peaks of nest predation and nest loss to eviction occurred at the same time (29 May), although a competing model suggested that the peak of nest loss due to eviction occurred five days earlier than the peak of mammalian nest predation.

Nest predation alone did not account for between-year dispersal (both from nests and clumps) of male and female flickers, perhaps because the risk of nest predation at specific nest sites and within clumps was not predictable from year to year. Within years, 73% of pairs switched nests, but dispersers did not have increased reproductive success compared to non-dispersers. A stressful immediate encounter with a predator

may trigger dispersal, despite this behaviour apparently not being beneficial. Pairs that encountered a model predator prior to egg-laying were no more likely to abandon their nest than pairs encountering a control model. Constraints or costs of finding and excavating a new cavity may discourage flickers from changing nest sites once a suitable location has been found.

Neither sex, age class, brood size, body size, nor body condition of the defending parent influenced nest defence behaviours, perhaps because the sexes are similar in size and have age-independent survival. It is possible that brood size is adjusted optimally by parents with respect to the number of young they can raise; if so, brood size may not influence parental investment into nest defence. When confronted with a model predator, older males blocked the cavity entrance more often than did younger males or females of any age. Blocking the entrance may be a learned behaviour; however, it is unclear why older females did not use this behaviour when defending their nest.

5.2 Conservation Implications

Flickers provide a "keystone structure" in this ecosystem (Tews et al. 2004) by excavating over 45% of the cavities that are subsequently used for nests and roost sites by over 15 species (Martin and Eadie 1999). Because of the dependence of secondary cavity nesters on flicker cavities it is likely that nest selection decisions by flickers could, similar to a top-down trophic cascade, filter down the nest web and influence nest predation or competition rates for generations of secondary cavity nesters.

In the last 40 years, the Northern Flicker population has been declining at a rate of 1.1% per year in Canada and 2.3% in North America (Moore 1995) and starlings have been considered to be a main cause (but see Koenig 2003). Starlings may have

indirect as well as direct impacts on the fitness of flickers, if flickers avoid competition with starlings by nesting in areas of higher predation risk (Chapter 2). Furthermore, the increasing forest harvest in central British Columbia and the recent infestation by the mountain pine beetle (*Dendroctonus ponderosae*) may reduce the coniferous forests important to nest predators, but at the same time may attract starlings into preferred open-ground habitat (Purcell et al. 2002).

Although my research was confined to the interior of British Columbia, squirrels and starlings are ubiquitous nest predators and competitors across North America (Ingold 1994; Bayne and Hobson 2002); therefore, my results are broadly applicable when trying to understand spatial and temporal patterns of predation. Sciurid predators in boreal and temperate forests are also common across much of Europe (Soderstrom et al. 1998), so my results may also apply in those areas. Current strategies of snag conservation for woodpeckers have focused simply on use, but have not examined reproductive success in relation to characteristics of snags (McClelland and McClelland 1999). My study identified several features of safe nest sites that could be incorporated into modern forestry practices (e.g., snag retention; Petit et al. 1985). For example, snags could be left approximately 250-300 m away from coniferous forest edges (Chapter 2) and small forest stands that are left on the landscape could contain approximately 30-35% conifers, which seemed the optimal balance between predation and competition (Chapter 2). The nest step would be to examine effects of these management strategies on nest survival of flickers and secondary cavity nesters using control areas for comparison. These guidelines could provide safe nesting locations for flickers and the secondary cavity nesters that use their cavities.

5.3 Future Directions

Determining whether flickers choose nest sites to mediate predation and/or competition is a logical extension of my study, as I have identified two processes that may influence nest selection in this population (Clark and Shutler 1999). To investigate nest selection, one should compare nest characteristics between random unused snags versus used snags and assess the availability of different snag types on the landscape. If flickers respond adaptively to predators or competitors they should prefer characteristics that reduce the risk of predation or competition. As starlings become increasingly common in western North America, the effects of nest competition could become more prevalent, so long-term data are required to test whether natural selection favours a shift in nest preferences of flickers. As suggested earlier, the effects of flicker nest choice on nest success of secondary cavity nesters should be investigated to determine whether similar patterns of predation and competition apply to the entire cavity-nesting community (Martin and Eadie 1999).

Studying the foraging behaviour (time budgets, habitat use) of common cavity nest predators would allow one to address the question of whether predators use search images to identify cavity nests and whether individual predators depredate cavity nests consistently (see for example, Pelech 1999). Examining the success of individual predators at finding and depredating nests within artificial snags (Petit et al. 1985) where characteristics such as nest height, concealment, and distance to conifers can be manipulated, would provide the most concrete evidence for the influence of nest characteristics on predation risk.

Other proximate mechanisms that could promote dispersal in this population need to be addressed, such as mate switching or ectoparasite densities in nests (Payne and Payne 1993). Experiments examining breeding dispersal after mate removal (forcing a mate switch) and after alteration of densities of nest parasites (e.g., fumigating nest sites) would test some of these hypotheses. Constraints in prospecting for new nest sites are still unknown, and we need a way to quantify costs of dispersal (e.g., survival and territory quality of dispersers versus non-dispersers) to solve the apparent paradox of dispersers having no greater nest success than non-dispersers. Expanding my study area or conducting similar population studies in multiple areas near Riske Creek (e.g., Winkler et al. 2004) to detect long-distance dispersers, would allow for a more accurate representation of the potential reproductive advantages or disadvantages of dispersing (Clark et al. 2004).

Finally, individual variation in nest defence needs to be explained. There may be a link between defence levels and nest characteristics themselves (e.g., nest height) such that nesting in a high-risk area may not be so costly if nest characteristics reduce costs of nest defence (Kleindorfer et al. 2005). These ideas may be tested more efficiently by varying heights of nest boxes and recording the subsequent responses of defending adults. To better interpret the relevance of particular defence behaviours, it would also be helpful to quantify costs and benefits to defending adults of particular defence behaviours such as cavity-blocking, perhaps by observing or videotaping encounters with natural predators.

LITERATURE CITED

Ackerman, J.T., J.M. Eadie, G.S. Yarris, D.L. Loughman, and M.R. McLandress. 2003. Cues for investment: nest desertion in response to partial clutch depredation in dabbling ducks. Anim. Behav. 66:871-883.

Aitken, K.E.H. and K. Martin. 2004. Nest cavity availability and selection in aspen-conifer groves in a grassland landscape. Can. J. For. Res. 34:2099-2109.

Aitken, K.E.H., K.L. Wiebe, and K. Martin. 2002. Nest-site reuse patterns for a cavity nesting bird community in interior British Columbia. Auk 119:319-402.

Andersson, M., C.G. Wiklund, and H. Rundgren. 1980. Parental defence of offspring: a model and an example. Anim. Behav. 28:536-542.

Badyaev, A.V. and J.D. Faust. 1996. Nest site fidelity in female wild turkey: potential causes and reproductive consequences. Condor 98:589-594.

Banks, A.J. and T.E. Martin. 2001. Host activity and the risk of nest parasitism by Brown-Headed Cowbirds. Behav. Ecol. 12:31-40.

Barclay, R.M.R. 1988. Variation in the costs, benefits, and frequency of nest reuse by Barn Swallows (*Hirundo rustica*). Auk 105:53-60.

Bayne, E.M. and K.A. Hobson. 2002. Effects of red squirrel (*Tamiasciurus hudsonicus*) removal on survival of artificial songbird nests in boreal forest fragments. Am. Midl. Nat. 147:72-79.

Bayne, E.M., K.A. Hobson, and P. Fargey. 1997. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. Ecography 20:233-239.

Beletsky, L.D. and G.H. Orians. 1991. Effects of breeding experience and familiarity on site fidelity in female Red-winged Blackbirds. Ecology 72:787-796.

Blancher, P.J. and R.J. Robertson. 1982. Kingbird aggression: does it deter predation? Anim. Behav. 30:929-936.

Blums, P., J.D. Nichols, M.S. Lindberg, J.E. Hines, and A. Medins. 2003. Factors affecting breeding dispersal of European ducks on Engure Marsh, Latvia. J. Anim. Ecol. 72:292-307.

Boulton, R.L., P. Cassey, C. Schipper, and M.F. Clarke. 2003. Nest site selection by Yellow-faced Honeyeaters *Lichenostomus Chrysops*. J. Avian Biol. 34:267-274.

Breitwisch, R. 1988. Sex differences in defence of eggs and nestlings by Northern

Mockingbirds, *Mimus polyglottos*. Anim. Behav. 36:62-72.

Burnham, K.P., D.R. Anderson, and K.P. Burnham. 1998. Model selection and
multimodal inference: a practical information-theoretic approach. Springer-
Verlag, New York.

Carignan, V. and M. Villard. 2002. Effects of variations in micro-mammal abundance
on artificial nest predation in conifer plantations and adjoining deciduous forests.
Forest Ecol. Manage. 157:255-265.

Cawthorn, J.M., D.L. Morris, E.D. Ketterson, and V. Nolan, Jr. 1998. Influence of
experimentally elevated testosterone on nest defence in Dark-eyed Juncos.
Anim. Behav. 56:617-621.

Chase, M.K. 2002. Nest site selection and nest success in a Song Sparrow population:
the significance of spatial variation. Condor 104:103-116.

Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Influence of body condition on
reproductive decision and reproductive success in the Blue Petrel. Auk
112:964-972.

Christman, B.J. and A.A. Dhondt. 1997. Nest predation in Black-capped Chickadees:
how safe are cavity nests? Auk 114:769-773.

Clark, R.G. and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-
site use by ducks? Ecology 80:272-287.

Clark, R.G., K.A. Hobson, J.D. Nichols, and S. Bearhop. 2004. Avian dispersal and
demography: scaling up to the landscape and beyond. Condor 106:717-719.

Compton, B.W., J.M. Rhymer, and M. McCollough. 2002. Habitat selection by wood
turtles (*Clemmys insculpta*): an application of paired logistic regression.
Ecology 83:833-843.

Cordero, P.J. and J.C. Senar. 1990. Interspecific nest defence in European Sparrows:
different strategies to deal with a different species of opponent? Ornis Scand.
21:71-73.

Cresswell, W. 1997. Nest predation: the relative effects of nest characteristics, clutch
size and parental behaviour. Anim. Behav. 53:93-103.

Crowder, L.B., D.D. Squires, and J.A. Rice. 1997. Nonadditive effects of terrestrial and
aquatic predators on juvenile estuarine fish. Ecology 78:1796-1804.

Dawson, R.D. and G.R. Bortolotti. 2003. Parental effort of American Kestrels: the role
of variation in brood size. Can. J. Zool. 81:852-860.

De Kiriline Lawrence, L. 1967. A comparative life-history study of four species of

woodpeckers. 1967. Ornithological Monographs, no. 5.

De Santo, T.L., M.F. Willson, K.M. Bartecchi, and J. Weinstein. 2003. Variation in nest sites, nesting success, territory size, and frequency of polygyny in winter wrens in northern temperate coniferous forests. Wilson Bull. 115:29-37.

Dinsmore, S.J., G.C. White, and F.L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476-3488.

Dobkin, D.S., A.C. Rich, J.A. Pretare, and W.H. Pyle. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97:694-707.

Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168-1170.

Dow, H. and S. Fredga. 1985. Selection of nest sites by a hole-nesting duck, the Goldeneye *Bucephala clangula*. Ibis 127:16-30.

Elchuk, C.L. and K.L. Wiebe. 2003. Ephemeral food resources and high conspecific densities as factors explaining lack of feeding territories in Northern Flickers (*Colaptes auratus*). Auk 120:187-193.

Evans, M.R., D.B. Lank, W.S. Boyd, and F. Cooke. 2002. A comparison of the characteristics and fate of Barrow's Goldeneye and Bufflehead nests in nest boxes and natural cavities. Condor 104:610-619.

Feare, C. J. 1984. The Starling. Oxford University Press, Oxford.

Filliater, T.S., R. Breitwisch, and P.M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter. Condor 96:761-768.

Forero, M.G., J.A. Donazar, J. Blas, and F. Hiraldo. 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. Ecology 80:1298-1310.

Frid, A. and L. Dill. 2002. Human-caused disturbance as a form of predation risk. Conservation Ecology 6:11 [online] URL: http://www.consecol.org/vol6/iss1/art11.

Ghalambor, C.K. and T.E. Martin. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. Behav. Ecol. 13:101-108.

Gill, S.A. and S.G. Sealy. 1996. Nest defence by Yellow Warblers: recognition of a brood parasite and an avian nest predator. Behaviour 133:263-282.

Gowaty, P.A. and J.H. Plissner. 1997. Breeding dispersal of Eastern Bluebirds depends

on nesting success but not on removal of old nests: an experimental study. J. Field. Ornithol. 68:323-330.

Grantner, A. and M. Taborsky. 1998. The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae). J. Comp. Physiol. B 168:427-433.

Green, A.J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473-1483.

Greenwood, P.J. and P.H. Harvey. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Syst. 13:1-21.

Greig-Smith, P.W. 1982. Dispersal between nest-sites by Stonechats (*Saxicola torquata*) in relation to previous breeding success. Ornis Scand. 13:232-238.

Griggio, M., G. Matessi, and A. Pilastro. 2003. Male Rock Sparrow (*Petronia petronia*) nest defence correlates with female ornament size. Ethology 109:659-669.

Gutzwiller, K.J. and S.H. Anderson. 1987. Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. Condor 89:534-548.

Haas, C.A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk 115:929-936.

Hamer, K.C. and R.W. Furness. 1993. Parental investment and brood defense by male and female Great Skuas *Catharacta skua* - the influence of food-supply, laying date, body size and body condition. J. Zool. 230:7-18.

Harvey, P.H., P.J. Greenwood, and C.M. Perrins. 1979a. Breeding area fidelity of Great Tits (*Parus major*). J. Anim. Ecol. 48:305-313.

Harvey, P.H., P.J. Greenwood, C.M. Perrins, and A.R. Martin. 1979b. Breeding success of Great Tits *Parus major* in relation to age of male and female parent. Ibis 121:216-219.

Hatch, M.I. 1997. Variation in Song Sparrow nest defence: individual consistency and relationship to nest success. Condor 99:282-289.

Hinch, S.G. and N.C. Collins. 1991. Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observations. Trans. Am. Fish. Soc. 120:657-663.

Holt, R.F. and K. Martin. 1997. Landscape modification and patch selection: the demography of two secondary cavity nesters colonizing clearcuts. Auk 114:443-455.

Hooge, P.N., M.T. Stanback, and W.D. Koenig. 1999. Nest-site selection in the Acorn Woodpecker. Auk 116:45-54.

Hoover, J.P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary Warbler. Ecology 84:416-430.

Hosmer, D.W. and S. Lemeshow. 2000. Applied Logistic Regression: Second Edition. John Wiley and Sons, Inc., New York.

Howlett, J.S. and B.J.M. Stutchbury. 1997. Within-season dispersal, nest site modification, and predation in renesting Hooded Warblers. Wilson Bull. 109:643-649.

Ingold, D.J. 1994. Influence of nest-site competition between European Starlings and woodpeckers. Wilson Bull. 106:227-241.

Jackson, W.M., S. Rohwer, and V. Nolan. 1989. Within-season breeding dispersal in Prairie Warblers and other passerines. Condor 91:233-241.

Julliard, R., R.H. McCleery, J. Clobert, and C.M. Perrins. 1997. Phenotypic adjustment of clutch size due to nest predation in the Great Tit. Ecology 78:392-404.

Kieffer, J.D. 1991. The influence of apparent predation risk on the foraging behavior of eastern chipmunks (*Tamias striatus*). Can. J. Zool. 69:2349-2351.

Kleindorfer, S., B. Fessl, and H. Hoi. 2005. Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. Anim. Behav.

Knight, R.L. and S.A. Temple. 1986a. Methodological problems in studies of avian nest defence. Anim. Behav. 34:561-566.

Knight, R.L. and S.A. Temple. 1986b. Nest defence in the American Goldfinch. Anim. Behav. 34:887-897.

Knight, R.L. and S.A. Temple. 1986c. Why does intensity of avian nest defence increase during the nesting cycle? Auk 103:318-327.

Koenig, W.D. 2003. European Starlings and their effect on native cavity-nesting birds. Conserv. Biol. 17:1134-1140.

Korpimäki, E. 1987. Selection for nest-hole shift and tactics of breeding dispersal in Tengmalm's Owls *Aegolius funereus*. J. Anim. Ecol. 56:185-196.

Krebs, C.J., S. Boutin, and R. Boonstra. 2001. Ecosystem Dynamics of the Boreal Forest: the Kluane Project. Oxford University Press, New York.

Lahti, D.C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biol. Conserv. 99:365-374.

Larivière, S. and F. Messier. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? Oikos 83:12-20.

Li, P. and T.E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405-418.

Lindberg, M.S. and J.S. Sedinger. 1997. Ecological consequences of nest site fidelity in Black Brant. Condor 99:25-38.

Martin, K. and J.M. Eadie. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecol. Manage. 115:243-257.

Martin, K. and A.G. Horn. 1993. Clutch defense by male and female Willow Ptarmigan *Lagopus lagopus*. Ornis Scand. 24:261-266.

Martin, K., K.E.H. Aitken, and K.L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. Condor 106:5-19.

Martin, T.E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473. *In* J.M. Hagan III and D.W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, D.C.

Martin, T.E. 1993. Nest predation and nest sites: new perspectives on old patterns. BioScience 43:523-533.

Martin, T.E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecol. Monogr. 65:101-127.

Martin, T.E. and P. Li. 1992. Life history traits of open- vs cavity- nesting birds. Ecology 73:579-592.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255-261.

Mazgajski, T.D. 2003. Nest site choice in relation to the presence of old nests and cavity depth in the starling *Sturnus vulgaris*. Ethol. Ecol. Evol. 15:273-281.

McClelland, B.R. and P.T. McClelland. 1999. Pileated Woodpecker nest and roost tress in Montana: links with old-growth and forest "health". Wildl. Soc. Bull. 27:846-857.

Møller, A.P. 1988. Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. Oikos 53:215-221.

Møller, A.P. 1989. Parasites, predators and nest boxes: facts and artifacts in nest box studies of birds? Oikos 56:421-423.

Montgomerie, R.D. and P.J. Weatherhead. 1988. Risks and rewards of nest defence by parent birds. Q. Rev. Biol. 63:167-187.

Moore, W.S. 1995. Northern Flicker: *Colaptes auratus*. *In* Poole, A. and Gill, F. [eds], The Birds of North America, No. 166. The Academy of Natural Sciences, Philadelphia; The American Ornithologist's Union, Washington, D.C.

Nams, V.O. 1997. Density-dependent predation by skunks using olfactory search images. Oecologia 110:440-448.

Nealen, P.M. and R. Breitwisch. 1997. Northern Cardinal sexes defend nests equally. Wilson Bull. 109:269-278.

Niemuth, N.D. and M.S. Boyce. 1995. Spatial and temporal patterns of predation of simulated Sage Grouse nests at high and low nest densities: an experimental study. Can. J. Zool. 73:819-825.

Nilsson, S.G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand. 15:167-175.

Nilsson, S.G. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. Auk 103:432-435.

Olendorf, R. and S.K. Robinson. 2000. Effectiveness of nest defence in the Acadian Flycatcher *Empidonax virescens*. Ibis 142:365-371.

Orrock, J.L., B.J. Danielson, and R.J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct cues of predation risk. Behav. Ecol. 15:433-437.

Parejo, D., E. Danchin, and J.M. Aviles. 2004. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? Behav. Ecol. 16:96-105.

Paton, P.W. 1994. The effect of edge on avian nest success: how strong is the evidence? Conserv. Biol. 8:17-26.

Pavel, V. and S. Bureš. 2001. Offspring age and nest defence: test of the feedback hypothesis in the Meadow Pipit. Anim. Behav. 61:297-303.

Payne, R.B. and L.L. Payne. 1993. Breeding dispersal in Indigo Buntings: circumstances and consequences for breeding success and population structure. Condor 95:1-24.

Pelech, S.A. 1999. Habitat use and nest searching success of red squirrels at a forest edge. M.Sc. thesis, University of British Columbia. Vancouver, B.C.

Peterson, B. and G. Gauthier. 1985. Nest site use by cavity-nesting birds of the cariboo parkland, British Columbia. Wilson Bull. 97:319-331.

Petit, D.R., K.E. Petit, T.C. Grubb, and L.J. Reichhardt. 1985. Habitat and snag selection by woodpeckers in a clear-cut: an analysis using artificial snags. Wilson Bull. 97:525-533.

Petit, K.E., L.J. Petit, and D.R. Petit. 1989. Fecal sac removal: do the pattern and distance of dispersal affect the chance of nest predation? Condor 91:479-482.

Pinkowski, B.C. 1977. Breeding adaptations in the Eastern Bluebird. Condor 79:289-302.

Powell, L.A. and L.L. Frasch. 2000. Can nest predation and predator type explain variation in dispersal of adult birds during the breeding season? Behav. Ecol. 11:437-443.

Pribil, S. and J. Picman. 1997. The importance of using the proper methodology and spatial scale in the study of habitat selection by birds. Can. J. Zool. 75:1835-1844.

Promislow, D.E., R. Montgomerie, and T.E. Martin . 1992. Mortality costs of sexual dimorphism in birds. Proc. Roy. Soc. Lond., Series B 250:143-150.

Purcell, K.L. and J. Verner. 1999. Nest predators of open and cavity nesting birds in Oak woodlands. Wilson Bull. 111:251-256.

Purcell, K.L., J. Verner, and S.R. Mori. 2002. Factors affecting the abundance and distribution of European Starlings at the San Joaquin experimental range. USDA Forest Service Gen. Tech. Rep. PSW-GTR-184.

Radford, A.N. and J.K. Blakey. 2000. Intensity of nest defence is related to offspring sex ratio in the great tit *Parus major*. Proc. R. Soc. Lond., Series B 267:535-538.

Rauter, C.M., H. Reyer, and K. Bollmann. 2002. Selection through predation, snowfall and microclimate on nest-site preferences in the Water Pipit *Anthus spinoletta*. Ibis 144:433-444.

Rendell, W.B. and R.J. Robertson. 1989. Nest-site characteristics reproductive success and cavity availability for Tree Swallows breeding in natural cavities. Condor 91:875-885.

Rising, J.D. and K.M. Somers. 1989. The measurement of overall body size in birds. Auk 106:666-674.

Shields, W.M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). Auk 101:780-789.

Short, L.L. 1982. Woodpeckers of the World. Delaware Museum of Natural History, Delaware.

Shutler, D. and R.G. Clark. 2003. Causes and consequences of Tree Swallow (*Tachycineta bicolor*) dispersal in Saskatchewan. Auk 120:619-631.

Sieving, K.E. and M.F. Willson. 1998. Nest predation and avian species diversity in northwestern forest understory. Ecology 79:2391-2402.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends Ecol. Evol. 13:350-355.

Slagsvold, T. and J.T. Lifjeld. 1989. Constraints on hatching asynchrony and egg size in Pied Flycatchers. J. Anim. Ecol. 58:837-849.

Soderstrom, B., T. Part, and J. Ryden. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. Oecologia 117:108-118.

Sonerud, G.A. 1985a. Nest hole shift in Tengmalm's Owl *Aegolius funerus* as defence against nest predation involving long-term memory in the predator. J. Anim. Ecol. 54:179-192.

Sonerud, G.A. 1985b. Risk of nest predation in three species of hole nesting owls: influence on choice of nesting habitat and incubation behaviour. Ornis Scand. 16:261-269.

Sproat, T.M. and G. Ritchison. 1993. The nest defence behavior of Eastern Screech-owls: effects of nest stage, sex, nest type and predator location. Condor 95:288-296.

Stanback, M.T. and A.A. Dervan. 2001. Within-season nest-site fidelity in eastern bluebirds: disentangling effects of nest success and parasite avoidance. Auk 118:743-745.

Steinhart, G.B., M.E. Sandrene, S. Weaver, R.A. Stein, and E.A. Marschall. 2004. Increased parental care cost for nest-guarding fish in a lake with hyperabundant nest predators. Behav. Ecol. 16:427-434.

Templeton, C.N. and W.M. Shriner. 2004. Multiple selection pressures influence Trinidadian Guppy (*Poecilia reticulata*) antipredator behavior. Behav. Ecol. 15:673-678.

Test, F.H. 1945. Molt in flight feathers of flickers. Condor 47:63-72.

Tews, J., U. Brose, V. Grimm, K. Tielborger, M.C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the important of keystone structures. J. Biogeogr.

31:79-92.

Thorson, J.M., R.A. Morgan, J.S. Brown, and J.E. Norman. 1998. Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. Behav. Ecol. 9:151-157.

Tolonen, P. and E. Korpimäki. 1995. Parental effort of kestrels (*Falco tinnunculus*) in nest defense: effects of laying time, brood size, and varying survival prospects of offspring. Behav. Ecol. 6:435-441.

Tryjanowski, P. and A. Golawski. 2004. Sex differences in nest defence by the Red-backed Shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. J. Ethol. 22:13-16.

Veen, T., D.S. Richardson, K. Blaakmeer, and J. Komdeur. 2000. Experimental evidence for innate predator recognition in the Seychelles Warbler. Proc. R. Soc. Lond. B 267:2253-2258.

Walters, E.L. and E.H. Miller. 2001. Predation on nesting woodpeckers in British Columbia. Can. Field-Nat. 115:413-419.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. J. Anim. Ecol. 71:424-437.

Wesolowski, T. 2002. Anti-predator adaptations in nesting Marsh Tits *Parus palustris*: the role of nest-site security. Ibis 144:593-601.

Wiebe, K.L. 2000. Assortative mating by color in a population of hybrid Northern Flickers. Auk 117:525-529.

Wiebe, K.L. 2001. Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? Auk 118:412-421.

Wiebe, K.L. 2003. Delayed timing as a strategy to avoid nest-site competition: testing a model using data from starlings and flickers. Oikos 100:291-298.

Wiebe, K.L. 2004. Innate and learned components of defence by flickers against a novel nest competitor, the European Starling. Ethology 110:1-13.

Wiebe, K.L. 2005. Asymmetric costs favor female desertion in the facultatively polyandrous Northern Flicker (*Colaptes auratus*): a removal experiment. Behav. Ecol. Sociobiol. 57:429-437

Wiebe, K.L. and C.L. Elchuk. 2003. Correlates of parental care in Northern Flickers *Colaptes auratus*: do the sexes contribute equally while provisioning young? Ardea 91:91-101.

Wiebe, K.L. and K. Martin. 1997. Effects of predation, body condition and temperature

on incubation rhythms of White-tailed Ptarmigan *Lagopus leucurus*. Wildlife Biology 3:219-227.

Wiebe, K.L. and T.L. Swift. 2001. Clutch size relative to tree cavity size in Northern Flickers. J. Avian. Biol. 32:167-173.

Wiklund, C.G. 1990. Offspring protection by Merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defense of young. Behav. Ecol. Sociobiol. 26:217-223.

Wiklund, C.G. 1996. Determinants of dispersal in breeding Merlins (*Falco columbarius*). Ecology 77:1920-1927.

Willson, M.F., T.L. De Santo, and K.E. Sieving. 2003. Red squirrels and predation risk to bird nests in northern forests. Can. J. Zool. 81:1202-1208.

Willson, M.F. and S.M. Gende. 2000. Nesting success of forest birds in southeast Alaska and adjacent Canada. Condor 102:314-325.

Winkler, D.W. 1992. Causes and consequences of variation in parental defense behavior by Tree Swallows. Condor 94:502-520.

Winkler, D.W., P.H. Wrege, P.E. Allen, T.L. Kast, P. Senesac, M.F. Wasson, P.E. Llambias, V. Ferretti, and P.J. Sullivan. 2004. Breeding dispersal and philopatry in the Tree Swallow. Condor 106:768-776.

Witkander, U., O. Olsson, and S.G. Nilsson. 2001. Annual and seasonal reproductive trends in the Lesser Spotted Woodpecker *Dendrocopus minor*. Ibis 143:72-82.