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Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition

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Abstract To date, most studies of nest site selection have failed to take into account more than one source of nest loss (or have combined all sources in one analysis) when examining nest site characteristics, leaving us with an incomplete understanding of the potential trade-offs that individuals may face when selecting a nest site. Our objectives were to determine whether northern flickers (*Colaptes auratus*) may experience a trade-off in nest site selection in response to mammalian nest predation and nest loss to a cavity nest competitor (European starling, *Sturnus vulgaris*). We also document within-season temporal patterns of these two sources of nest loss with the hypothesis that flickers may also be constrained in the timing of reproduction under both predatory and competitive influence. Mammalian predators frequently depredated flicker nests that were: lower to the ground, less concealed by vegetation around the cavity 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. Flickers may thus face a trade-off in nest site selection with respect to safety from predators or competitors. Models suggested that peaks of nest predation and nest loss to eviction occurred at the same time, although a competing model suggested that the peak of nest loss to starlings occurred 5 days earlier than the peak of mammalian predation. Differences in peaks of mammalian predation and loss to starlings may constrain any adjustment in clutch initiation date by flickers to avoid one source of nest loss.

Keywords Primary excavator · European starling · Mammalian nest predator · Nest survival

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Introduction

Nest predation is a major source of nest loss in avian systems, accounting 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). In general, 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's nests, but most have only examined nest site selection in response to one nest predator or have failed to consider responses to different predators. Birds contend with a rich guild of predators each with differing search strategies and differing affinities for prey types, potentially leading to trade-offs in nest selection to avoid different predators (Sih et al. 1998). Furthermore, competition for nest sites, where offspring are killed or removed from the nest, result in a situation similar to predation, but this has rarely been examined in conjunction with loss to predators. Here we document nest site selection and temporal aspects of northern flicker (*Colaptes auratus*), a primary cavity excavator, nesting in relation to nest loss to mammals and an avian competitor, the European starling (*Sturnus vulgaris*).

Cavity nesters may experience relatively low nest predation rates compared to open-cup nesting species (Martin and Li 1992), but nest predation still remains the largest source of nest loss for cavity nesters, although in some cases competition may also account for a significant source of nest loss (Tracy 1938), and therefore both competition and predation have a great potential to influence nest site 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). We overcame this potential pitfall by evaluating 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 favor nests higher off the ground (nest height hypothesis; Li and Martin 1991). For cavity-nesting species, the diameter of the 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 1985; Pelech 1999). If predators encounter a high density of nests it may lead to either development of a search image, or increased predator search effort and result in higher predation risk for nests in high density clusters compared to nests in low density cluster (Niemuth and Boyce 1995). In general, the risk of nest predation will depend on (1) within and between year variation in predator abundance or behavior and (2) predator species richness (Filliater et al. 1994).

To determine if competitors exert any 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 some 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). In this paper we use the term competition to describe interactions between European starlings and northern flickers; however, cavity kleptoparasitism (after Kappes 1997; Mazgajski 2003) may be a more accurate term to describe the situation when a starling benefits after usurping a cavity from a flicker.

Temporal patterns of nest predation have not been as widely examined 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 (Dinsmore et al. 2002) and ptarmigan (*Lagopus lagopus*; K. Martin unpublished data). Peak periods of predation may occur because predators develop a search image for prey items or else switch food items throughout the season depending upon energetic requirements or food availability. We are aware of one study that has examined temporal patterns of nest predation in a primary cavity-nesting species (Sandstrom 1991).

Plasticity of clutch initiation date (CID) may allow nesting birds to avoid temporal peaks of nest predation during the breeding season and nest when it should be significantly safer (Wiebe 2003). Although changing laying date may be a way to temporally avoid one predator, if the new laying 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 our study area include: red squirrels (12 predation attempts captured on videotape, 2 successful), long-tailed weasel (*Mustela frenata*; observed once), marten (*Martes americana*; observed once), black bears (*Ursus americanus*) occurring approximately ten times in the past 7 years (K.L. Wiebe unpublished data). Other possible predators in the area include northern flying squirrel (*Glaucomys sabrinus*), and deer mice (*Peromyscus maniculatus*; Walters and Miller 2001), but we have never observed these directly preying on eggs. Because red squirrels are a main nest predator on our study site, we hypothesized that predation risk would be highest at: (1) nests that are 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) nests with large clutches (i.e., increased olfactory cues), and (5) nests with a high density of active cavities surrounding them. Furthermore, we hypothesized that flickers may experience 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 nest sites and thus increase predation risk on nests at certain times during the breeding season.

If starlings have nest preferences, they may compete more intensely for flicker nests with those attributes. Specifically, European starlings may prefer higher (Nilsson 1984) and less concealed (T. Mazgajski personal communication) cavities. Lastly, we also expected peaks in nest loss due to starlings at the beginning of the flicker breeding season when starlings are prospecting for suitable nests and most takeovers usually occur (Wiebe 2003).

We 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. We also used program MARK to model temporal trends of flicker nest loss spanning our 7-year dataset, considering depredation and competition separately.

Materials and methods

Study area and general methods

The study site near Riske Creek, British Columbia (51°52′N, 122°21′W) encompasses approximately 100 km^2 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*) for nesting, and continuous forests of Douglas fir (*Pseudotsuga menziesii*) and hybrid spruce (*Picea engelmannii* × *glauca*) also occur.

Every year since 1998, the area has been surveyed in spring to check old cavities for new breeding pairs and to search for newly excavated cavities because flickers tend to reuse old cavities more often than other woodpeckers. Tape-recorded territorial playback calls were also used to localize flicker territories and subsequently nest sites. Once clutches were complete, a small door was cut into the side of the nest tree for access to adults, eggs and nestlings (Wiebe 2001). Each nest site was visited every few days (average length between visits was 4.2 days) with a ladder, flashlight and mirror to monitor nest contents.

We analyzed characteristics of nests with three possible fates. Successful nests had at least one young fledged. We 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 predators. Whereas mammals tend to leave eggshell fragments in the cavity, starlings remove flicker eggs and deposit them outside the nest (Wiebe 2003). We defined a nest as having been lost to starlings when the following chronological sequence of events occurred: (1) flickers began laying and were observed in the nest cavity, and (2) we found a breeding starling in the nest cavity on a subsequent visit or starling nesting material (green vegetation, which is a unique nesting characteristic of this species) was inside the cavity.

Nest and site characteristics

We measured attributes of nest sites and their surroundings once chicks fledged to avoid excessive disturbance to the nesting pair. 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. We measured nest characteristics, based on relevant nest predation literature, at five spatial scales that may affect nest predation risk: (1) cavity scale—cavity dimensions, (2) nest tree scale—measurements associated with the tree itself, (3) a small nest tree plot—a 2-m radius surrounding the nest tree, (4) a large nest tree plot—an 11.2-m radius (0.04 ha) surrounding the nest tree and (5) the landscape level—beyond 11.2 m (Table 1).

Nest comparison analysis

Two separate analyses of successful versus depredated (hereafter predation analysis) and evicted nest sites (hereafter evicted 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. 1). If a cavity was used more than once in the 7-year period one nest attempt was selected at random to avoid pseudoreplication. Where possible, nests that were lost to eviction were left in the analysis to maximize the sample size available for comparison with successful nests. We 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 evicted analysis included 213 successful and 18 nests lost to eviction.

Stepwise logistic regression was used in both analyses and included the following independent 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 radius of the cavity entrance and 2-m radius of the nest tree, number of aspen, conifers and cavities within the 11.2-m radius of the nest tree, distances to dry, coniferous forest, wet edge, the percentage conifer content of the active nest clump and the size of the nesting forest clump. Cavity age was not included in the analyses as other work showed that predation risk was not associated with nest reuse (K. L. Wiebe et al., in review) and we wanted to limit the number of variables included in the analysis. We used a correlation analysis to reduce problems of multicollinearity between selected variables. A preliminary correlation analysis revealed that no pairs of variables exceed the usual multicollinearity standard of $r \geq 0.70$ (Compton et al. 2002) and the models did not have inflated slope coefficients and standard errors (Hosmer and Lemeshow 2000) that would suggest multicollinearity. 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

Table 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) Percentage of vegetation concealment within 1 m radius surrounding and perpendicular to the cavity entrance[b]
Tree	Cavity height from ground (m) Number of cavities, excluding the active flicker cavity
2-m radius surrounding nest tree	Percentage of vegetation ground cover[b]
11.2-m radius surrounding nest tree[a]	Number of aspen Number of conifers Number of other cavities Number of used cavities (only in 2003 and 2004)[c]
Landscape	Distance to dry grassland edge (m) Distance to wet edge (m) Distance to continuous coniferous edge (m) Clump area (ha)[d] Percentage of conifer content of the clump[b]

[a] British Columbia Ministry of Forests Inventory Standard (Aitken et al. 2002)

[b] Visual estimate by Ryan J. Fisher

[c] Twelve minutes observations were done at each nest site 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 we did not check cavities specifically for eggs

[d] We used digital air photos of the study area taken from 2000 and rendered in ArcView (v. 3.2, 1999) with nest points overlaid to calculate an exact estimate of clump area

predation analysis is approximately 19–1 and 18–1 for the eviction analysis, with a ratio of 20–1 being preferred for logistic regression analysis (minimum 10–1; 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). We 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). We only conducted surveys for other active cavity nesters within 11.2 m of flicker nest sites in 2003 and 2004, therefore we analyzed this variable separately using non-parametric tests.

Program MARK nest survival analysis

We analyzed daily probability of nest survival using two separate program MARK analyses in order to evaluate temporal variation in nest loss, as well as effects of CID and clutch size (CS) (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 to 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, abandon-

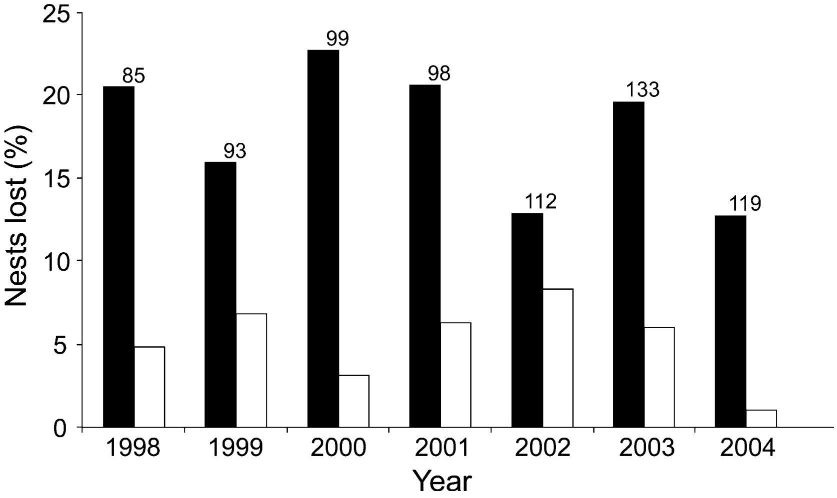

Fig. 1 Total percentage of northern flicker (*Colaptes auratus*) nests that were lost to predators (*filled bars*) or eviction (*open bars*) from 1998 through 2004 at Riske Creek, British Columbia. Sample size of total nests found each year is above the *bars*

ment for inexplicable reasons) except nests abandoned due to human disturbance ($<2\%$ of all nests lost). We also included three covariates in the models: CID and CS, plus CID squared. We modeled linear as well as quadratic time trends over the breeding season, as well as basic models of year differences and constant nest survival.

Since we wanted to examine the temporal effects of both types of nest loss (predation and eviction), we conducted a second nest survival analysis. 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 in order to examine time trends of nest predation and nest eviction. We 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. We 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. We used AIC corrected (AICc) for small sample sizes to select the most parsimonious model in each analysis (Burnham and Anderson 1998).

Results

Nest and site characteristics

A general description of flicker nest characteristics is in Table 2. The predation analysis suggested that nests with lower cavity height, less vegetation cover within 1 m radius of the cavity and 2 m radius of the tree base, closer to a coniferous edge, and in clumps with a higher conifer content had a higher probability of predation (Table 3; Figs. 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 $\chi^2=4.273$, $P=0.83$). 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 3, Fig. 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 $\chi^2=8.449$, $P=0.39$). For each significant nest trait (Table 2) we tested directly whether there were differences in these nest characteristics between depredated and evicted nests using non-parametric Mann–Whitney U tests. There were no significant differences between depredated and evicted nests sites in cavity height ($U=816.5$, $P=0.55$), percentage vegetation concealment within 1m of the nest cavity ($U=892.0$, $P=0.99$) and within 2 m 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 ($U=378.5$, $P<0.001$). There were significant differences in the number of active cavities surrounding successful, depredated, and evicted nests (Kruskal Wallis $\chi^2=13.872$, $df=2$, $P=0.001$). Post-hoc comparisons revealed that nests that were evicted by starlings had approximately one more active cavity nest surrounding them than did either depredated (Bonferroni adjusted Mann–Whitney $U=53$, $P<0.001$) or successful (Bonferroni adjusted Mann–Whitney $U=253$, $P=0.002$) nests, however this was based on a small sample of only eight evicted nest sites.

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; Fig. 4) plus effects of CS and CID as covariates (Table 4). Daily nest survival rates increased

Table 2 General description 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 other cavities	1	1
	Percentage of vegetation cover 1 m	4	10
Small plot	Percentage of vegetation cover 2 m	22	23
Large plot	Number of aspen	7.1	6.6
	Number of conifer	2.6	5.1
	Number of cavities	1	2
Landscape	Distance to dry edge (m)	11.2	13.9
	Distance to wet edge (m)	180.8	276.2
	Distance to coniferous edge (m)	253.7	202.6
	Clump size (ha)	13.8	103.4
	Percentage of conifer content of forest clump	31	33

Table 3 Variables that were significant predictors of nest failure in separate logistic regression analyses on depredated nests and nests lost to eviction by starlings

	B	SE	Wald	*P*
Predation				
Height (m)	−0.406	0.130	9.782	0.002
Percentage of vegetation cover 1 m	−0.098	0.034	8.219	0.004
Percentage of vegetation cover 2 m	−0.021	0.009	6.053	0.014
Distance to coniferous edge (m)	−0.003	0.001	8.123	0.004
Percentage of conifer content of forest clump	0.009	0.004	4.009	0.045
Eviction				
Distance to coniferous edge (m)	0.002	0.001	3.469	0.063
Percentage of conifer content in forest clump	−0.044	0.016	7.462	0.006

with increasing CS ($\hat{\beta}=0.351$, 95% CI: 0.169–0.532), but decreased with later CIDs ($\hat{\beta}=-0.268$, 95% CI: −0.509– −0.028). The best overall model was ($\hat{\beta} \pm$ SE): Logit (daily nest survival estimate) = $(4.96 \pm 3.79) - (0.07 \pm 0.263\ \mathrm{T}) + (0.002 \pm 0.004\ \mathrm{TT}) + (0.351 \pm 0.093\ \mathrm{CS}) - (0.268 \pm 0.123\ \mathrm{CID})$. There was little support for annual differences in daily nest survival (Table 4).

The second MARK analysis suggested that rates of depredation and eviction on flicker clutches followed the same quadratic time trend throughout the breeding season (Table 5; Fig. 4a); however, the second most parsimonious model suggested that peak eviction occurred 5 days earlier than peak predation (Table 5; Fig. 4b).

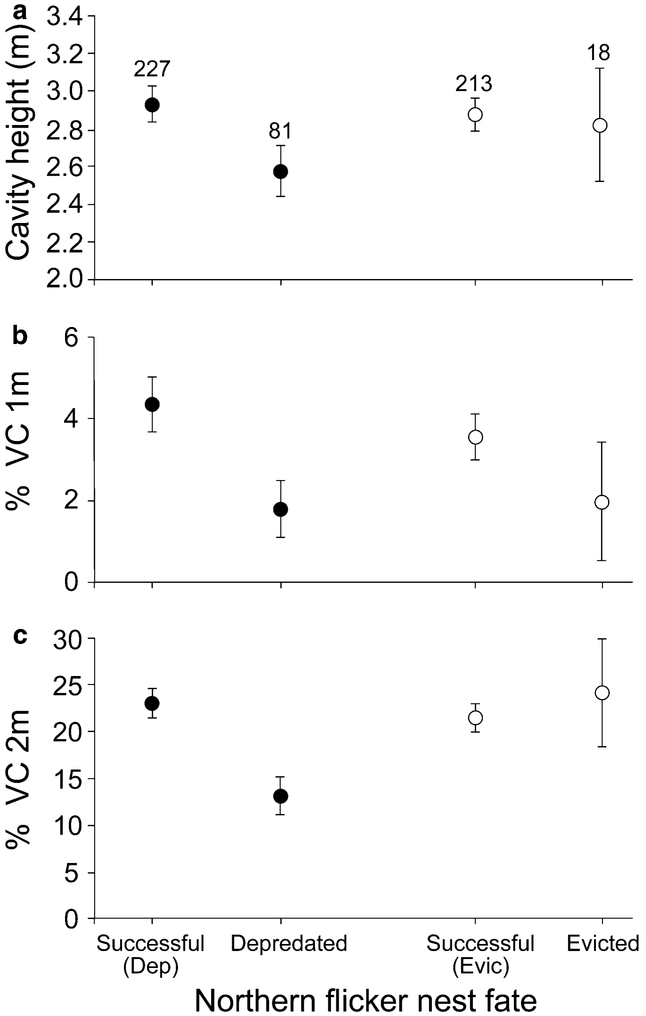

Fig. 2 Characteristics of successful and unsuccessful nests that were either depredated or evicted: **a** cavity height, **b** vegetation cover within 1 m radius of cavity entrance (%VC 1 m) and **c** vegetation cover within 2 m radius around tree base (%VC 2 m) (means ± SE). Sample sizes are presented above each *error bar*. Note that "Successful(dep)" and "Successful(evic)" correspond to the random subsample of successful nests used in the depredation (*filled circles*) or eviction (*open circles*) comparison, respectively

Discussion

Nest and site characteristics

Several cavity and tree characteristics were significant predictors of whether a nest would be depredated (Table 3). Despite a mean difference of approximately 0.5 m between successful and depredated nests, higher nests were more successful (Fig. 2). Our estimate of the height of successful nests may be biased low if extremely high nests that we could not monitor (> 8 m) were successful. However, the fraction of nests that we could not monitor was < 2%. Our finding 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), *P. palustris* (Wesolowski 2002), 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), *T. bicolor* (Rendell and Robertson 1989), *S. vulgaris*, *P. caeruleus*, and *P. palustris* (Nilsson 1984), *Bucephala islandica* (in nest boxes and natural cavities; Evans et al. 2002). As summer progresses, squirrels may switch from arboreal feeding strategies to more ground based foraging (Pelech 1999), and therefore, a small height advantage may be significant in deterring 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, the 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. Our finding that concealment of the nest by vegetation can reduce pre-

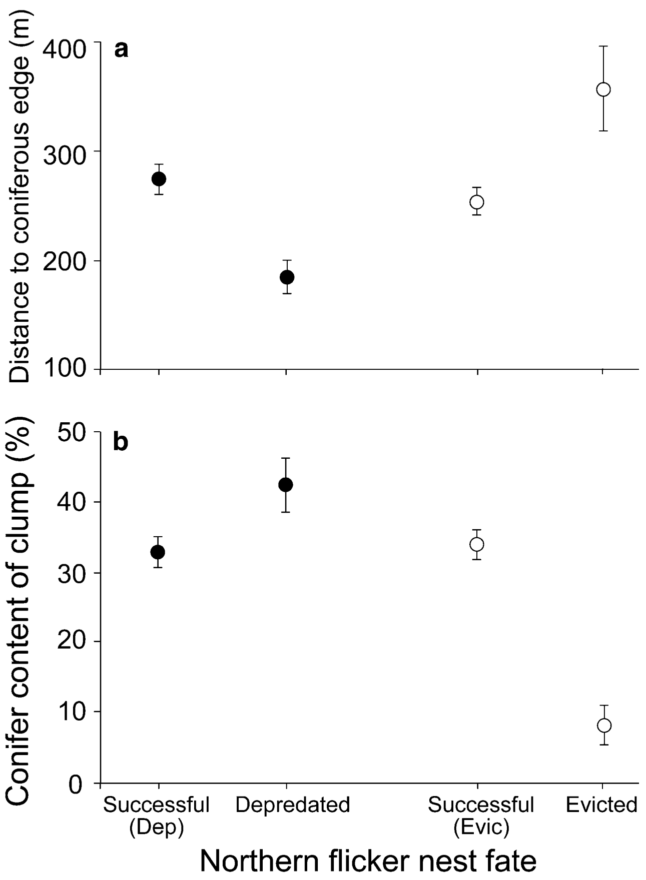

Fig. 3 **a** Distance to coniferous forest edge from nest cavity and **b** percentage conifer content of the nesting clump which significantly predicted both predation and eviction (means ± SE). Note that "Successful(dep)" and "Successful(evic)" correspond to the random subsample of successful nests used in the depredation (*filled circles*) or eviction (*open circles*) comparison, respectively. Sample sizes in each cateory are the same as in Fig. 2

dation either through camouflage of the nest itself or by increasing or encumbering predator search effort is also consistent with other studies (Martin 1992).

At the mid-sized plot, nests that were lost to starlings had significantly more active nests surrounding them than either successful or depredated nests. Starlings searching for nest sites may cue in on tree clumps with high activity of cavity nesters and then may compete with flickers there for a cavity. Similar to brown-headed cowbirds *Molothrus ater* (a brood parasite) that use host activity to find nests (Banks and Martin 2001), starlings may concentrate their search for nests in areas of high activity. Starlings may prefer to nest in colonies; 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).

We 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 our 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 unpublished data), similar to other published studies outside our study area (e.g., Bayne et al. 1997). Although we did not quantify squirrel abundance, it is reasonable to assume that squirrel activity would be higher in coniferous stands compared to deciduous stands and that bird nests in the former would be exposed to increased predation risk (Bayne et al. 1997). Conversely, starlings appeared to avoid stands dominated by conifers. This corresponds well with other studies that have found that starlings nest within 500 m of suitable foraging areas which are typically open grasslands (Feare 1984) and nest in stands with high edge-to-interior ratios (Dobkin et al. 1995). At a study site near Riske Creek, Peterson and Gauthier (1985) found that starlings nested on the edge of forest patches, while flickers nested in sparsely treed groves. On our study area, Aitken and Martin (2004) found that starling nests were closer to grassland edges than random points.

Opposing pressures by multiple predators on prey behavior 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 behavior. 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. However, 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 of both predators and competitors on flicker nest survival.

Temporal patterns of nest loss

Daily nest survival was characteristically high as is typical for a cavity-nesting species (i.e., greater than 0.90, see Willson and Gende (2000) for a list of daily Mayfield nest survival rates for cavity nesters), and never dropped below 0.98 in any of the models we tested. The rate of nest loss peaked in mid May and there was some support (i.e., ΔAICc < 2) for the model where starling evictions peaked about 5 days earlier than predation (Fig. 4b). The peak date of starling loss calculated by program MARK (24 May—day 144) was

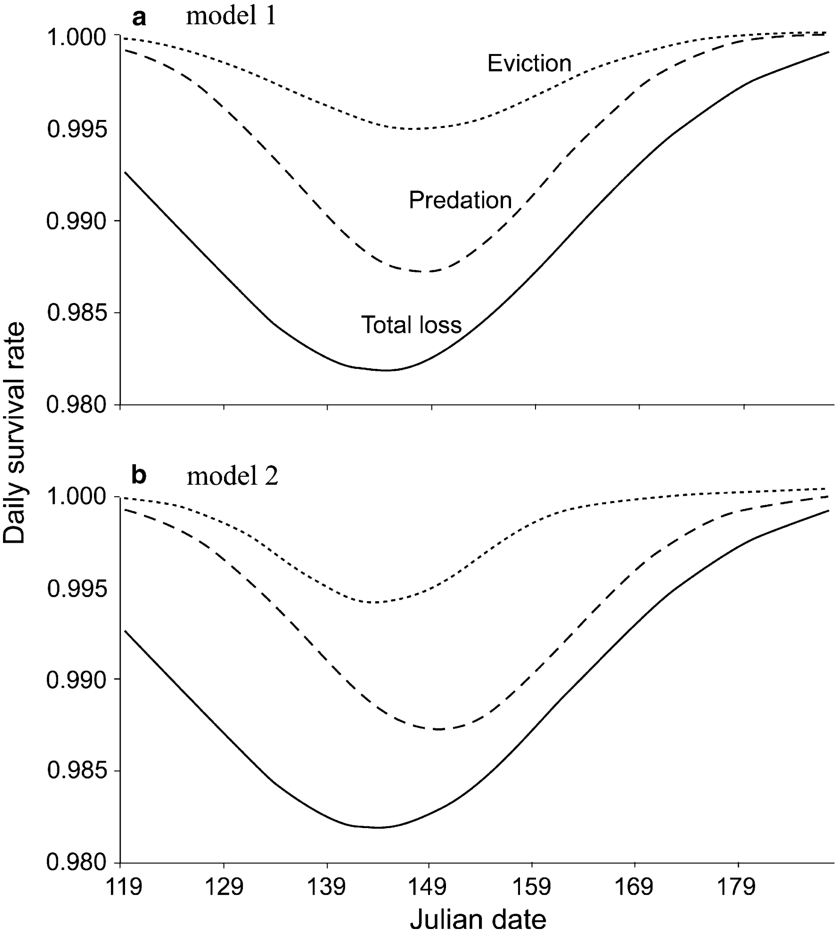

Fig. 4 Daily nest survival probability through time as affected by mammalian predation (*dotted lines*) and eviction (*dashed line*) by European starlings, predicted by two models. The effects of predation and eviction occur at the same time in (**a**) model 1 (S(g + T + TT)) but are displaced 5 days in (**a**) model 2 (S(g + T + TT + g*TT))—see Table 4 for explanation of model terms. The temporal pattern of all sources of nest loss combined (*solid lines*) (see Table 4) is included for comparison

similar to peak dates of evictions found by Wiebe (2003). However, we may have underestimated the risk of eviction early in spring because we could not detect all early evictions when flickers were defending a cavity but had not yet laid eggs. It is also possible that we 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 we found most evicted and depredated nests. By the time of peak nest loss to predation on day 149, 79% of nests had been initiated, with a mean CID of 138 (± 12.34 SD), providing support for the hypothesis that predators may not begin to actively search for nests until most of the population had 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 source such as eggs and fungi in mid summer and then harvesting and caching cones in late summer, potentially creating the period of peak nest predation that we observed.

Table 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 less than 0.01 are not presented; however, we do present the model of constant daily nest survival, S(.), for comparison

Model[a]	AICc[b]	ΔAICc[c]	w_i[d]	*K*[e]
S (T + TT + CS-CID)	1,018.95	0.00	0.67	5
S (T + TT + CS)	1,021.01	2.07	0.24	3
S (T + CS-CID)	1,024.24	5.29	0.05	4
S (CS)	1,025.90	6.96	0.02	2
S (CS-CID)	1,026.91	7.97	0.01	3
S (T + CS)	1,026.98	8.03	0.01	3
S (.)	1,042.47	23.52	0.00	1

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

[b] Akaike's Information Criterion with correction for small sample sizes

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

[d] Estimates of the likelihood of the model given the observed data; all models sum to 1.00.

[e] Number of estimable parameters in the models

Delaying nesting to avoid competition by starlings may not increase reproductive success if delayed nests then have a higher risk of being depredated. Given that predation currently causes more nest loss than eviction (Fig. 1), it may not be advantageous for flickers in our population to alter CIDs in response to this nest competitor (Wiebe 2003). The overall decline in CS with laying date also favors early nesting (Wiebe 2003).

Table 5 Models analyzed comparing timing of mammalian nest depredation and nest eviction due to European starlings. Table headings are the same as Table 4. Four models with weights <0.001 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), a linear time trend (T), and a quadratic time trend (TT)

Effects of clutch size and clutch initiation date

Because larger clutches are exposed to predation for longer periods of time and larger clutches may attract attention from predators, it is generally thought 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 therefore CS may not influence predation risk directly. Since CS is positively associated with female age (K.L. Wiebe, unpublished data) higher investment in nest defense by more experienced birds may increase nest security.

Nests that were initiated later in the breeding season had increased probability of loss (Table 3). In this population, there is a strong negative correlation between CS and CID (Wiebe 2003) and perhaps late-hatched fledglings have lower reproductive value as is observed in other woodpeckers (Witkander et al. 2001), suggesting that factors such as nest abandonment or reduced parental care, as a result of energetic demands on parents that attempt to renest, may reduce nest survival late in the season regardless of nest predation or competition.

General conclusions

To date, most studies of the success of bird nests have combined all sources of loss (but see Rauter et al. 2002). Similar to other nest predation studies, we documented some nest features that appear to offer safety from mammalian predation risk with no trade-off with respect to security from starlings. However, we 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 our 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 site choice at large scales may have greater consequences for reproductive success than constraints of cavity or snag type at the microhabitat scale.

Clark and Shutler (1999) suggested that nest loss may be 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 our study area compared to sciurid nest predators and destroy fewer nests than squirrels. 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.

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