RESOURCE SELECTION PLASTICITY AND COMMUNITY RESPONSES TO EXPERIMENTAL REDUCTION OF A CRITICAL RESOURCE

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Abstract. Resource selection plasticity and behavioral dominance may influence the ability of a species to respond to changes in resource availability, particularly if dominant species have highly specialized resource requirements. We examined the response of several dominant and subordinate cavity-nesting species to a reduction in the availability of an essential resource (nesting cavities) using the novel experimental approach of blocking the entrances to high-quality cavities. We monitored nest abundance on seven treatment and 13 control sites (aspen groves in a grassland matrix) in British Columbia, Canada, for two years pretreatment (2000–2001), two years during treatment (2002–2003), and two years posttreatment (cavities reopened; 2004–2005). At the community level, nest abundance declined by 50% on treatment sites following cavity blocking and returned to pretreatment levels following cavity reopening. Nest abundance of European Starlings (*Sturnus vulgaris*), a dominant secondary cavity-nester (SCN), declined by 89% and failed to recover posttreatment. Conversely, nest abundance of Mountain Bluebirds (*Sialia currucoides*; a subordinate SCN) increased following cavity blocking and remained high following reopening. Tree Swallows (*Tachycineta bicolor*) were unaffected by cavity blocking. We suggest that starlings, while being the dominant SCN, may be limited by availability of suitable nest sites, whereas bluebirds may be limited by starling abundance. We propose that plasticity in nest site preferences of subordinate cavity-nesters may enable them to contend with natural variation in availability of critical resources, such as nest cavities and food, in addition to coping with interspecific competition. This is the first community-level, multiyear study involving manipulation of nest site availability via experimental cavity blocking.

Key words: cavity-nesting birds and mammals; dominant and subordinate species; European Starling; Mountain Bluebird; natural cavities; nest site limitation; plasticity in resource selection; resource limitation; resource quality; secondary cavity-nesters; Sialia currucoides; Sturnus vulgaris.

INTRODUCTION

Cavity-nesting communities, which are structured hierarchically based on production of and competition for suitable cavities, consist of species that vary in their degree of nest site specialization and dominance (Martin and Eadie 1999). Nesting resources may be limited or unpredictable for these species (Newton 1994) and individuals that are able to exploit a range of nest sites may have greater opportunities for breeding than individuals that are restricted in their nest site requirements. Secondary cavity-nesting species, which cannot excavate their own cavities, rely on cavities created by woodpeckers or on a limited number of naturally occurring non-excavated cavities (Aitken and Martin 2007). Although landscape-level cavity abundance may be relatively stable, there may be considerable local variation in cavity availability and quality (Aitken and Martin 2004). Thus, cavity-nesting communities provide an opportunity to study the effects of changes in resource availability on species across a range of resource acquisition strategies.

Resource selection plasticity and behavioral dominance may influence the ability of a species to respond to temporal and spatial changes in resource availability, particularly if dominant species have highly specialized resource requirements (Pimm and Pimm 1982, Palmer 2003). Subordinate species with more generalized resource preferences than dominant species may be better able to withstand stochasticity in resource availability (Pimm and Pimm 1982, Palmer 2003). Additionally, plasticity in nest site selection may allow individuals to utilize a broader range of habitat types and to reduce nest predation and interspecific competition (Albano 1992, Cuervo 2004, Forstmeier and Weiss 2004, Eggers et al. 2006). Thus, the extent to which natural and human-induced environmental variability impact community structure and stability may be influenced by the ecological plasticity of component species (Brown et al. 2001, Hooper et al. 2005, Richmond et al. 2005).

Cavity density in mature aspen (*Populus tremuloides*) groves in the Cariboo-Chilcotin region of British

Columbia, Canada, averages 16 cavities/ha with overall occupancy rates of 35–44% (Aitken 2002, Aitken and Martin 2004). However, occupancy rates of individual cavities vary, because some cavities are occupied every year whereas others are occupied only sporadically (Aitken et al. 2002). Among high-quality cavities (those occupied annually or biannually), cavity-nesters exhibited preferences related to cavity age, size, and proximity to edge (Aitken et al. 2002, Aitken and Martin 2004). Thus, although nest sites may appear to be abundant, individual species preferences may influence true availability of the nest site resource.

Using a cavity-blocking experiment, we altered availability of high-quality cavities in order to: (1) examine changes in nesting abundance at the cavity-nester community and species levels in response to changes in the availability of an essential resource, tree cavities; and (2) determine whether secondary cavity-nesters in a natural landscape with an apparent abundance of cavities were, in fact, nest site limited. We predicted that if nest site availability were limited for some species in this community, nest abundance of these species would be correlated with changes in cavity abundance. Finally, we addressed whether previous occupation by the European Starling (*Sturnus vulgaris*), an introduced secondary cavity-nester, influenced the future probability of occupation by other cavity-nesting species.

METHODS

Study area

Fieldwork was conducted on Becher's Prairie, near the community of Riske Creek (51°52′ N, 122°21′ W, 850–1000 m elevation), in interior British Columbia (BC), Canada. The area consists of a matrix of mature trembling aspen (*Populus tremuloides*) groves and mixed coniferous forest interspersed with small lakes and grassland. Research was conducted in 20 aspen groves (0.1–1.7 ha each), spaced an average of 84 m (range 16–222 m) from the nearest grove or forest, and dominated by trembling aspen, with varying amounts of lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*). Additional details for study sites and design are given in Aitken and Martin (2004) and Martin et al. (2004).

Six of the 10 most common cavity-nesting species in the area nest almost exclusively in aspen groves (European Starling *Sturnus vulgaris*, Tree Swallow *Tachycineta bicolor*, Mountain Bluebird *Sialia currucoides* (see Plate 1), Northern Flicker *Colaptes auratus*, Bufflehead *Bucephala albeola*, and American Kestrel *Falco sparverius*; Aitken 2007). European Starlings, which were introduced to North America in the late 1800s, arrived in British Columbia in 1945 and became established in interior BC in the early 1950s (Peterson and Gauthier 1985, Campbell et al. 1997).

Nest monitoring and cavity-blocking experiment

We utilized a replicated before–after-control–impact (BACI) experimental design (Underwood 1992, 1994), in which we monitored cavities for two years prior to treatment (cavity blocking), two years during treatment, and two years following cavity reopening on seven treatment sites and 13 control sites. All previously active nest trees were marked with numbered aluminum tags and previously active cavities were assigned identifying numbers as part of a larger cavity-nester study operating on the study area since 1995 (Martin and Eadie 1999). From 1 May to 31 July 2000–2005, previously active and newly excavated cavities were monitored approximately twice per week. Cavities within reach of a ladder (≤5.2 m above ground) were checked with a flashlight and mirror and were considered active nests if they contained at least one egg or nestling (or pups in the case of small mammals; see Plate 1). Cavities >5.2 m above ground were assessed for activity using behavioral cues. For example, high cavities were considered to contain an active nest if we observed an adult entering and remaining inside the cavity or poking its head out on more than two occasions, or observed evidence of nestling presence (adult entering with food or removing a fecal sac; begging nestlings). Thus we may have underestimated the use of high cavities, particularly if nests failed early in the nesting cycle (e.g., during incubation). However, cavities higher than 5.2 m made up 20% of those in the area (Aitken and Martin 2004), and therefore we feel that even if we missed some nests in high cavities, it would not significantly affect our results, particularly because the most abundant species in the area (starlings, bluebirds, swallows, and flickers) prefer relatively low cavities (Aitken and Martin 2004).

In April 2002, prior to the start of the breeding season, we blocked all high-occupancy cavities (those that had been occupied in the previous two years; Aitken et al. 2002) within reach of a ladder (≤5.2 m) on treatment sites using plastic garden mesh stapled over the cavity entrance. We blocked 35 of 79 cavities (44%) on treatment sites, representing 30–80% of cavities in each grove. Of the 35 cavities blocked in 2002, 29% (n = 10) were occupied by European Starlings in the year prior to blocking, 14% (n = 5) were occupied by Tree Swallows, 11% each were occupied by Mountain Chickadees (*Poecile gambeli*; n = 4) and Northern Flickers (n = 4), 6% (n = 2) were occupied by Mountain Bluebirds, 3% each by American Kestrels (n = 1) and Red-breasted Nuthatches (*Sitta canadensis*; n = 1), and 23% (n = 8) were empty (but occupied in 2000). Overall, cavity blocking resulted in a 46% decrease in cavity density, from a pretreatment mean of 27.3 cavities/ha to 14.8 cavities/ha during treatment. On treatments sites, blocked cavities did not differ significantly from unblocked cavities (not used in the previous two years) in internal depth, entrance area, tree diameter at breast height (dbh), or distance to nearest edge, but tended to be lower above ground and wider internally (Table 1). Mean height above ground, internal depth and width, and entrance area of blocked cavities fell within the range of those used by the most abundant

TABLE 1. Characteristics of blocked cavities (used in previous two years) and unblocked cavities (not used in previous two years) on treatment sites in 2002.

Variable	Blocked cavities			Unblocked cavities			t	df	P
	Mean	SE	n	Mean	SE	n			
Cavity height above ground (m)	2.8	0.17	35	3.5	0.30	44	−1.9	77	0.06
Internal depth (cm)	23.8	2.6	30	25.2	4.4	35	−0.28	63	0.8
Internal width (cm)	14.7	1.1	34	12.3	0.84	37	1.8	69	0.08
Entrance area (cm²)†	27.9	3.0	35	28.2	3.9	36	−0.45	77	0.7
dbh (cm)	33.6	1.6	35	34.6	1.5	44	1.4	75	0.2
Nearest edge (m)	9.0	1.2	35	6.6	1.2	42	0.46	69	0.6

Note: Means were compared using independent samples *t* tests.

† Data were log-transformed where necessary to meet assumptions of normality.

species on our study sites (starlings, bluebirds, tree swallows, flickers, and red squirrels; Martin et al. 2004). We removed the blocking material in late July 2003, and continued to follow nesting on all 20 sites during the 2004 and 2005 breeding seasons.

Four blocked cavities were repeatedly chewed open and used for nesting or roosting by red squirrels (*Tamiasciurus hudsonicus*) in 2002. They were reblocked at the end of the breeding season in 2002, but two were repeatedly chewed open again in 2003 (one was used for roosting by a red squirrel, while the other was used for nesting by a Tree Swallow). Two additional blocked cavities were repeatedly chewed open in 2003, one of which was used for roosting by an unidentified small mammal, and the other was used for nesting by a Tree Swallow. As well, woodpeckers (one Northern Flicker, one Red-naped Sapsucker *Sphyrapicus nuchalis*) excavated new entrances to two blocked cavities, which they subsequently used for nesting.

Data analysis

We examined the effect of cavity blocking on nest abundance of all cavity-nesting birds and mammals, and three SCN species for which sufficient data were available (≥10 nests/year): European Starling, Mountain Bluebird, and Tree Swallow. We used generalized linear mixed-effects models using a penalized quasi-likelihood method of parameter estimation in the statistical package R (glmmPQL; R Version 2.4.0; R Development Core Team 2006). GlmmPQL is an appropriate statistical analysis when dependent data follow a Poisson distribution, as was the case with our nest abundance data (Breslow and Clayton 1993, Nelson and Leroux 2006). Treatment type (cavity blocking or control) and period ("pre-blocking," 2000–2001; "during blocking," 2002–2003; and "post-blocking," 2004–2005) were fixed effects, site was a random effect, and nest abundance was the dependent variable.

We also present transition data showing across-year use of cavities to address the question of whether previous occupancy influenced cavity selection, and whether occupancy by starlings influenced cavity use following reopening. Cavity occupancy transitions were examined for three periods: pre-blocking (2000–2001),

during blocking (2001–2002 and 2002–2003 grouped), and post-blocking (2003–2004 and 2004–2005 grouped). All cavities for which there were two consecutive years of data and for which there was an occupant in the first year were examined. Each pair of occupancy observations was treated separately. Cavities that were newly excavated or that were destroyed between years or blocked were not included.

RESULTS

Effect of cavity blocking on nest abundance

Cavity blocking resulted in a significant decline in community-level nest abundance on treatment sites (Table 2a). Total abundance of bird and mammal nests on treatment sites decreased by 42% in 2002 and a further 13% in 2003, resulting in a total decrease in nest abundance of 50% over the two treatment years (Fig. 1a). Total nest abundance returned to near pretreatment levels in 2004 (Fig. 1a). The mean number of species nesting on treatment sites per year declined from nine in the pre-blocking period to seven during blocking and returned to nine following cavity reopening, while the mean number of species nesting on control sites did not change throughout the study (average 10 species/year). American Kestrels, Red-breasted Nuthatches, and red squirrels nested on treatment sites in both years prior to cavity blocking but not during the treatment period (kestrels) or only in 2002 (nuthatches, squirrels). Kestrels and squirrels nested on control sites throughout the study, whereas nuthatches did not nest on control sites after 2001.

The decline in total nest abundance after cavity blocking was largely accounted for by a significant decline in nests of the European Starling (the most abundant secondary cavity-nester) on treatment sites (Table 2b). Starling nests decreased by 72% on treatment sites in the first year after blocking (2002) and a further 60% in 2003, resulting in a total decrease of 89% in abundance in the two years cavities were blocked (Fig. 1b). There was a corresponding increase in starling nest abundance on control sites in the second treatment year (2003; Fig. 1b). After blocking materials were removed from cavities, starling nest abundance did not return to

TABLE 2. Generalized linear mixed model predicting abundance of total bird and mammal cavity nests, and nests of European Starling, Mountain Bluebird, and Tree Swallow in relation to treatment type (control or cavity blocking) and period (pre-blocking, during blocking, or post-blocking).

	a) Total birds and mammals			b) European Starling		
Parameter	Estimate ± SE	t	P	Estimate ± SE	t	P
Intercept	1.06 ± 0.20	5.21	<0.0001	−1.30 ± 0.54	−2.42	0.02
Treatment, control vs. blocking	0.47 ± 0.25	1.90	0.07	1.37 ± 0.63	2.17	0.04
Period, pre-blocking vs. during blocking	0.58 ± 0.15	3.85	0.0002	1.52 ± 0.35	4.40	<0.0001
Period, post-blocking vs. during blocking	0.50 ± 0.15	3.26	0.002	−0.15 ± 0.46	−0.33	0.7
Pre-blocking period × control treatment	−0.58 ± 0.18	−3.22	0.002	−1.31 ± 0.39	−3.36	0.001
Post-blocking period × control treatment	−0.55 ± 0.18	−2.99	0.004	−0.05 ± 0.50	−0.10	0.9

Notes: For nest types of all taxa, df = 96 for all parameters except treatment type (control vs. blocking), where df = 18. Parameters were calculated in relation to Treatment type = "Blocking" and Period = "During blocking." For example, the significant positive parameter estimates for total bird and mammal nests in the pre-blocking and post-blocking periods indicate that nest abundance was significantly higher in those two periods than during blocking. A significant negative interaction effect indicates that nest abundance was higher on control sites relative to treatment sites during blocking than pre-blocking or post-blocking. Site was included in the model as a random effect.

pretreatment levels, and remained lower on treatment sites than on controls in both 2004 and 2005.

Cavity blocking had a significant positive effect on Mountain Bluebird nest abundance, with an increase in nest numbers beginning in the second year of cavity blocking and continuing until the end of the study (Table 2c, Fig. 1c). Tree Swallow nest abundance was not significantly affected by cavity blocking (Table 2d, Fig. 1d).
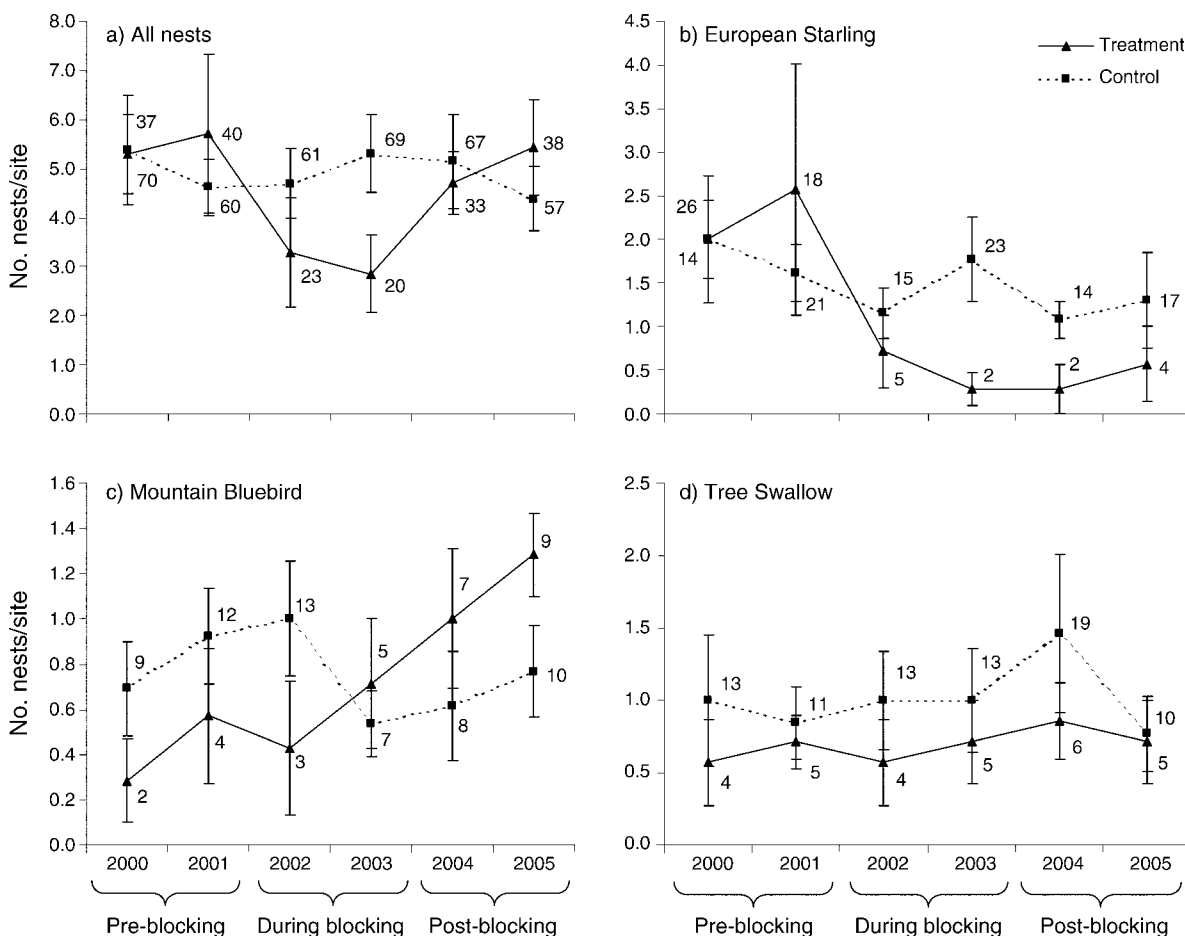

FIG. 1. Nest abundance (mean ± SE) of (a) all cavity-nesting birds and mammals, (b) European Starlings, (c) Mountain Bluebirds, and (d) Tree Swallows on seven treatment sites (cavity blocking; solid line) and 13 control sites (dotted line) at Riske Creek, British Columbia, Canada. Sample sizes shown beside points indicate the total sample of nests.

Table 2. Extended.

c) Mountain Bluebird			d) Tree Swallow		
Estimate ± SE	t	P	Estimate ± SE	t	P
−0.62 ± 0.36	−1.73	0.09	−0.66 ± 0.45	−1.45	0.2
0.17 ± 0.43	0.39	0.7	0.23 ± 0.55	0.42	0.7
−0.29 ± 0.39	−0.73	0.5	0.00 ± 0.35	0.00	1.0
0.69 ± 0.32	2.20	0.03	0.20 ± 0.34	0.59	0.6
0.34 ± 0.45	0.74	0.5	−0.08 ± 0.41	−0.19	0.8
−0.80 ± 0.39	−2.02	0.05	−0.09 ± 0.39	−0.23	0.8

Influence of starling occupancy on subsequent cavity use

Of 286 cavities in the data set (treatments and controls combined), 23% ($n = 66$) were occupied by starlings at least once between 2000 and 2005, and 57 of those were available in at least one year following starling occupancy (e.g., were not blocked or destroyed). Of those, 58% ($n = 33$) were subsequently used for nesting by another species, including American Kestrel, Bufflehead, Northern Flicker, Tree Swallow, bushy-tailed woodrat (*Neotoma cinerea*), Mountain Bluebird, red squirrel, and Northern Saw-whet Owl (*Aegolius funereus*). Among cavities that were occupied by starlings, the percentage used for nesting in the following year by starlings (intraspecific reuse), by other species (interspecific reuse), or that remained empty varied among years and between treatment and control sites (here, reuse refers to occupancy of a cavity two years in a row, not necessarily by the same individuals; Fig. 2a). On treatment sites, the percentage of cavities that remained empty after occupancy by starlings increased across the study period, whereas the percentage that were reused by starlings decreased. On control sites, however, the percentage of starling cavities that were not used in the following year remained at ~20% throughout the study, whereas starling reuse of cavities increased from 59% to 74% during the treatment period. Interspecific reuse of cavities previously used by starlings varied considerably throughout the study, from 0% to 12% on treatment sites and 10% to 40% on controls (Fig. 2a). Conversely, among cavities that were occupied by species other than starlings, there was little variation in intraspecific or interspecific cavity reuse across years (Fig. 2b). However, the percentage of cavities that remained empty after occupancy by species other than starlings decreased during the cavity-blocking period on both treatment and control sites (Fig. 2b).

Of 12 starling cavities that were blocked in 2002 and that survived to 2004, four were used by other species in 2004 (one Mountain Bluebird, two Northern Flickers, one red squirrel), and six were used by other species in 2005 (two Mountain Bluebirds, three Northern Flickers, one Tree Swallow). Starlings did not use reopened cavities in 2004, and used only two in 2005.

DISCUSSION

At the community level, cavity-nesting bird and mammal populations decreased following cavity blocking and returned to pretreatment levels following cavity reopening, suggesting that the cavity-nesting community as a whole was limited by cavity abundance. However, species-level resistance to fluctuations in resource availability appeared to play a role in driving the community-level response. Species with generalist nest cavity preferences, such as Mountain Bluebirds and Tree Swallows, displayed high resistance to changes in cavity abundance following the experimental decrease in cavity availability, whereas the most dominant, specialist cavity-nester, the European Starling, displayed low resistance and resilience to cavity blocking. Generalist species may be better able to withstand stochasticity in resource availability than specialists (Pimm and Pimm 1982, Palmer 2003), whereas specialists may put more effort into acquiring a limited number of higher quality resources.

Response of European Starlings to cavity blocking

Abundance of starling nests declined significantly immediately after cavity blocking and did not recover in the two years after cavities were reopened. Interestingly, all seven starling nests in our treatment sites in 2002 and 2003 were in the only remaining cavities with characteristics similar to cavities previously occupied by starlings on those sites (K. E. H. Aitken and K. Martin, *unpublished data*). Although starlings usurp cavities from other species when nest sites are limited (Lindell 1996, Ingold 1998, Wiebe 2003), the fact that starlings did not evict occupants from the remaining unblocked cavities on our treatment sites suggests that starlings considered most of those cavities unsuitable for nesting. As well, we observed a slight increase in starling nest abundance on nearby control sites in the second treatment year, but did not see an increase in starling nest abundance on other study sites in the area, which were monitored as part of a long-term study in the region (K. Martin, *unpublished data*). Thus, it appears that starlings selected the few suitable unblocked cavities on treatment sites and, once those were occupied, a few

Occupant in year 2:　□ Same species　■ Other species　■ Empty

Treatment sites　　　　　　　　　　　　Control sites

a) Cavities occupied by starlings in year 1

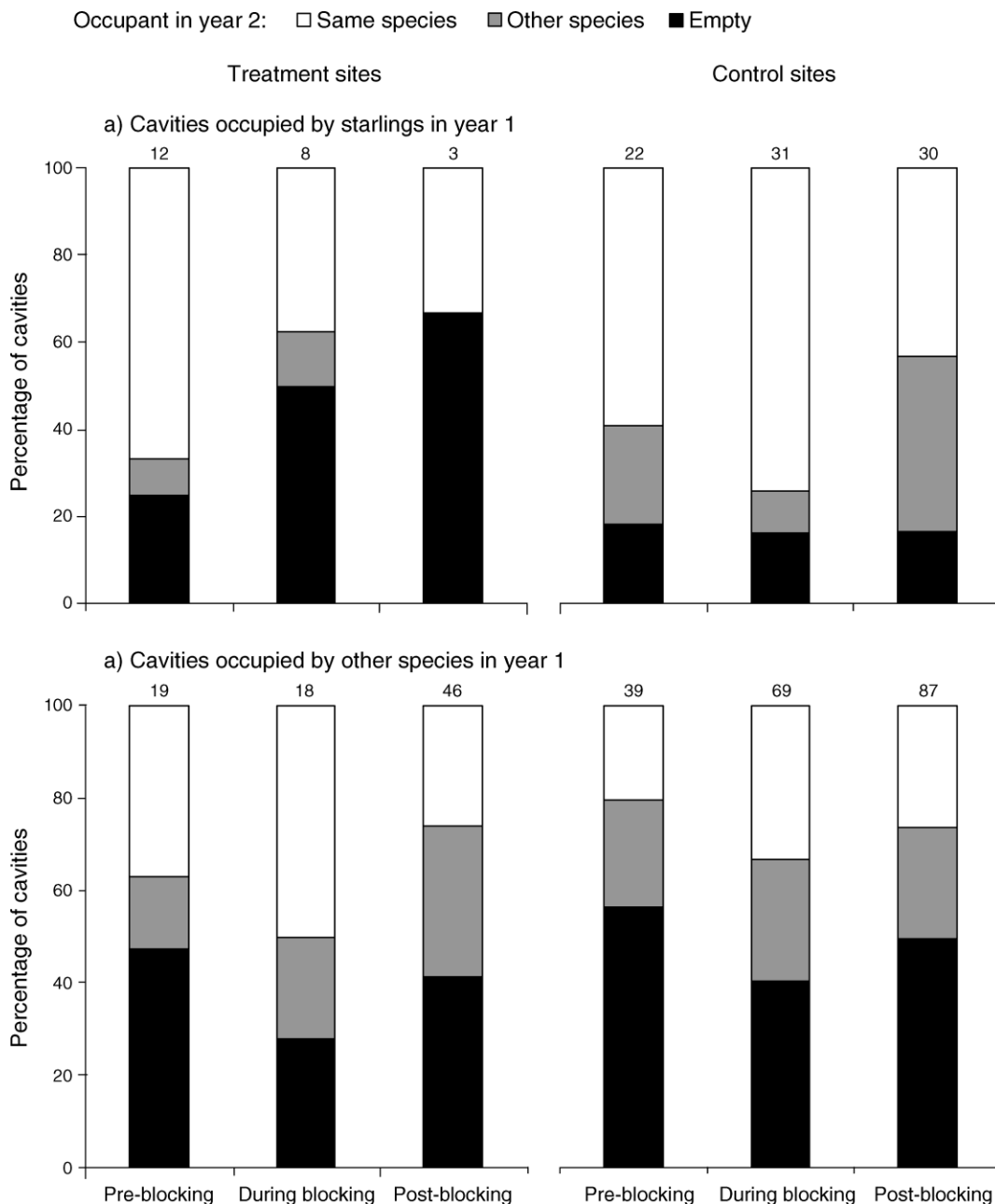a) Cavities occupied by other species in year 1

FIG. 2. Cavity occupancy transitions across consecutive years in relation to the species identity of the previous occupant. Bars represent the percentage of cavities occupied in year 1 by (a) starlings and (b) other species that were reused by the same species, were used by other species, or that remained empty in the following year. Reuse refers to occupancy of a cavity two years in a row, not necessarily by the same individuals. Numbers above bars indicate the total number of cavities occupied by starlings or other species that were available in the following year (e.g., were not blocked or destroyed). The pre-blocking period is 2000–2001, during blocking is 2001–2002 and 2002–2003 combined, and post-blocking is 2003–2004 and 2004–2005 combined.

starlings moved to other groves and others may simply have chosen to forego breeding.

Although starlings are considered nest site generalists because they have adapted successfully to nesting in both natural and human-made structures, nest site selection studies suggest that they have specialized nest site preferences. In Poland, starlings had stronger

preferences for nest cavities based on tree species, height above ground, and cavity entrance shape than did most other species in the community (Wesolowski 1989). Starlings in The Netherlands and Sweden preferred cavities that were large internally (van Balen et al. 1982, Carlson et al. 1998). Earlier, we found that starlings preferred nest sites that were larger internally, closer to

grassland edge, and in trees with only one cavity (Aitken and Martin 2004). Starlings in urban areas of Ontario used a smaller range of human-made structures and a narrower range of cavity characteristics than did another introduced secondary cavity-nester, the House Sparrow (*Passer domesticus*; Savard and Falls 1981). Lohmus and Remm (2005) suggested that availability of high-quality nest sites, as opposed to total cavity abundance, might limit some populations of secondary cavity-nesters. Our results suggest that starling populations may be limited by the availability of suitable cavities with a relatively narrow range of preferred characteristics.

Studies have noted a delayed response of some secondary cavity-nesters to changes in nest site availability (Brawn and Balda 1988), particularly among species that prospect for nest sites in the previous year (Eadie and Gauthier 1985, Stutchbury and Robertson 1987, Holt and Martin 1997, Poysa and Poysa 2002). Nonbreeding starlings (floaters) prospect for cavities for the following year by examining cavities occupied by conspecifics, particularly during the nestling period (Tobler and Smith 2004). This may explain the sustained negative impact of cavity blocking on starling nest abundance. Floaters that prospected for cavities on our treatment sites in 2001 (prior to cavity blocking) may have overestimated cavity availability for the following year, whereas birds prospecting in 2003 may have underestimated cavity availability for 2004. Additionally, because starlings are semicolonial and may use conspecific breeding activity as an indicator of nest site suitability (Tobler and Smith 2004), the low densities of breeders on the treatment sites in 2002 and 2003 may have dissuaded other starlings from returning to those sites in subsequent years, regardless of cavity availability in 2004 and 2005.

Response of Mountain Bluebirds and Tree Swallows to cavity blocking

Overall, Mountain Bluebird and Tree Swallow nest abundances were not affected negatively by the experimental reduction in cavity availability in this study. Both species are secondary cavity-nesters that co-occur with a range of other medium-sized cavity-nesting species in a variety of habitats throughout North America and display generalist nest site preferences (Robertson et al. 1992, Power and Lombardo 1996). In addition to excavated tree cavities, Mountain Bluebirds and Tree Swallows in our study area used non-excavated holes in broken tree limbs, hollow stumps, and crevices behind bark, as well as cavities in downed trees, cracks in boulders, and even a metal bridge piece for nesting (Martin et al. 2004, Aitken and Martin 2007). Swallows are considerably smaller than starlings, enabling them to use smaller cavities and thus reducing overlap in nest site requirements with starlings (Martin et al. 2004). Plasticity in nest site selection may have enabled Mountain Bluebirds and Tree Swallows to resist or

PLATE 1. (Top) A female Mountain Bluebird (*Sialia currucoides*) photographed near Riske Creek, British Columbia, Canada. Bluebirds are secondary cavity nesters, nesting in cavities excavated by woodpeckers or in naturally occurring non-excavated cavities. Photo credit: K. E. H. Aitken. (Bottom) K. E. H. Aitken checks a cavity in a dead aspen tree for nesting activity. Cavities were checked with a small telescoping mirror and a flashlight. Photo credit: K. Martin.

respond positively to the experimental changes in cavity availability in our study.

Foraging territory selection may also have influenced Mountain Bluebird response to cavity blocking. Bluebirds defend foraging territories adjacent to or near their nests sites, and also display nest site fidelity (Power and

Lombardo 1996; K. Martin, *unpublished data*). Thus, bluebirds returning to treatment sites in 2002 after cavities were blocked may have faced a trade-off between reestablishing their previous foraging territory but using an unblocked, possibly lower quality cavity, or moving to a different grove to obtain a higher quality cavity but having to acquire a new foraging territory.

Role of interspecific dominance in response of species to cavity blocking

Cavity blocking resulted in an increase in Mountain Bluebird nest abundance on treatment sites in the second year of the experiment and continued for at least two years after cavities were reopened. At the same time, there was a slight decline in bluebird nest abundance on control sites. The increase in bluebird abundance on treatment sites and decrease on controls corresponded with the decrease in starling abundance on treatment sites and slight increase on controls. This suggests that bluebird populations may be limited by starling presence, either through aggressive interactions or through exploitation competition for cavities (Ingold 1994, Sara et al. 2005). A combination of these factors probably influences the ability of bluebirds to secure nest sites in our study area. Starlings initiate nesting ~1–2 weeks earlier, on average, than do bluebirds on our sites (K. Martin, *unpublished data*), which may preempt bluebirds from obtaining some cavities. As well, starlings destroy or usurp nests of other cavity-nesters (Lindell 1996, Ingold 1998, Wiebe 2003). Previous studies have showed that the presence of starlings may influence nest site selection and timing of breeding by some native cavity-nesters (Kerpez and Smith 1990, Pell and Tidemann 1997, Ingold 1998, Fisher and Wiebe 2006). For example, Davis et al. (1986) found that starlings exclude bluebirds from potential nest sites through their earlier timing of breeding, but did not observe starlings directly evicting bluebirds from nests. When nesting in areas with European Starlings, Eastern Bluebirds (*Sialia sialis*) nested in cavities with smaller entrances than in areas without starlings (Pinkowski 1976). Mountain Bluebirds shifted to smaller and deeper cavities after starlings became established in central British Columbia in the 1950s (Peterson and Gauthier 1985). Plasticity in nest site selection and nesting phenology may allow bluebirds to coexist with and avoid direct competition with starlings.

Starlings are considered to be aggressive competitors in North America, Australia, and other regions where they have been introduced, with potentially detrimental effects on populations of native cavity-nesters (Kerpez and Smith 1990, Cabe 1993, Pell and Tidemann 1997). However, starlings may not be as adaptable and resilient as they are generally considered, given recent declines in starling populations in Europe, possibly due to changes in agriculture and loss of foraging habitat (Rintala et al. 2003, Svensson 2004, Laiolo 2005, Robinson et al. 2005). A review of North American Breeding Bird Survey and Christmas Bird Count trends found no evidence that starlings have severely impacted populations of cavity-nesters since their introduction (Koenig 2003). Pimm and Pimm (1982) suggested that behaviorally dominant species are more likely to be affected by disturbance than are subordinates, if the dominant species is restricted to higher quality resources while the subordinates are capable of using poorer resources. Our results suggest that plasticity in nest site preferences of native cavity-nesting species and inflexibility in starling nest site preferences may enable the coexistence of starlings with native species.

Experiments on population limitation in cavity-nesters

To our knowledge, the cavity-blocking experiment presented here is the first involving a replicated before–after-control–impact (BACI) design with multiple treatment and control sites, several years of data, and involving multiple species. Most studies of population limitation in cavity-nesters involve addition or removal of nest boxes, and very few studies have experimentally reduced or increased the availability of natural cavities. Blanc and Walters (2008) used metal restrictor plates to exclude Northern Flickers from using or enlarging Red-cockaded Woodpecker (*Picoides borealis*) cavities, but did not see a significant reduction in nest abundance of flickers, as most birds simply switched to using the remaining cavities. They did, however, observe a reduction in nesting abundance of large secondary cavity-nesters (American Kestrel and Eastern Screech Owl *Otus asio*). A few studies found that removal of all snags in experimental plots resulted in a reduction in cavity-nester breeding densities, but in these studies tree removal is confounded with cavity availability (Scott 1979, Raphael and White 1984, Lohr et al. 2002). Only two previous studies that we are aware of involved community-level cavity-blocking experiments, but both of those lacked long-term pre- and posttreatment data on more than one site (Brush 1983, Waters et al. 1990). Cavity-blocking experiments, while logistically more difficult than nest box experiments, may provide a more accurate reflection of population responses to variation in resource availability and thus deserve consideration by researchers examining population limitation in cavity-nester communities.

Ecological plasticity may allow species to withstand or even benefit from environmental stochasticity and to cope with interspecific competition (Ostfeld and Keesing 2000, Moreno et al. 2001, Yang 2004). However, plastic or generalist species may face trade-offs between using abundant but low-quality resources vs. more rare high-quality resources (Abrams 1990). For secondary cavity-nesters such as Mountain Bluebirds and Tree Swallows, selecting an abundant but low-quality cavity may reduce competition and energy spent on searching for a nest site, but may also result in lower reproductive success if that cavity is more vulnerable to predation, is not close to optimal foraging habitat, or has poor thermal

qualities (Slagsvold 1986, Sedgeley 2001, Lohmus 2003, Lohmus and Remm 2005). Conversely, secondary cavity-nesters that select a more rare but higher quality cavity may suffer reproductive costs if they expend more energy in locating or defending that nest site than in egg-laying, incubation, or parental care (Duckworth 2006). Cavity-nesters with less plastic nest site preferences or in habitats with few cavities may simply defer breeding if suitable high-quality nest sites are not available (Holt and Martin 1997), which appeared to be the case with starlings in our study. Further studies on trade-offs in resource availability and quality for cavity-nesters, and resource partitioning by cavity-nesters, will allow for a better understanding of the mechanisms of species coexistence in these communities.

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