Fire in the boreal forest: Proximate effects on reproduction and long-term consequences for territory occupancy of American kestrels

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Abstract: There is currently a great deal of interest in documenting habitat use of birds in the boreal forest, especially in response to disturbances such as harvesting and forest fires. Studies have shown that some avian species are much more common in recently burned areas, whereas others are absent. Despite this, we know little about the immediate effect of a large forest fire, and its considerable alteration of habitat, on birds during a single breeding season. In 1995, a 72,000-ha forest fire in our study area gave us the opportunity to assess the effects of fire on reproduction of American kestrels (Falco sparverius) in comparison to an adjacent control area. In addition, we also examined territory occupancy by kestrels in the burned and control areas 8 y following the fire. We found no immediate effect of the fire on body condition of adult kestrels, their ability to hatch eggs, or to fledge at least one young. Birds breeding in the area that burned, however, did fledge fewer offspring per nest, and these nestlings had reduced body mass compared to control nests, possibly because of an immediate reduction in available prey following the fire. Nonetheless, given the profound alteration of habitat following the fire, the fact that any birds remained to continue breeding is remarkable. Territory occupancy of the burned area in 2003 was similar to 1995; the year of the fire, but occupancy in the adjacent control area declined during this period. It therefore appears that the control area is becoming a less suitable habitat for kestrels as the forest continues to mature, whereas the burned area is still providing viable habitat for kestrels. We present evidence suggesting that some of the differences in occupancy between the control and burned area may be due to fewer nest predators in the burned area in 2003.

Keywords: American kestrels, boreal forest, Falco sparverius, forest fires, prey abundance, reproductive success, territory occupancy.

Résumé: Il existe présentement un grand intérêt à documenter l'utilisation de l'habitat par les oiseaux dans la forêt boréale, particulièrement à la suite de perturbations telles la coupe ou les feux. Des études ont montré que certaines espèces d'oiseaux étaient beaucoup plus abondantes dans les aires récemment brûlées alors que d'autres en étaient absentes. Cependant, nous avons peu d'information sur les effets immédiats d'un grand feu de forêt sur les oiseaux et l'altération considérable qu'il cause à l'habitat à l'intérieur d'une même saison de reproduction. En 1995, un feu a brûlé 72 000 ha de forêt dans notre aire d'étude ce qui nous a donné l'opportunité d'étudier les effets du feu sur la reproduction de la crécerelle d'Amérique (Falco sparverius) en comparant avec une aire adjacente non brûlée. Nous avons de plus examiné l'occupation du territoire par les crécerelles dans les aires brûlée et non brûlée huit ans après le feu. Nous n'avons trouvé aucun effet du feu sur la condition corporelle des crécerelles adultes, leur capacité à amener leurs œufs jusqu'à l'éclosion ou au moins un jeune jusqu'à l'envol. Les oiseaux se reproduisant dans l'aire brûlée ont cependant eu moins de jeunes par nid qui ont atteint l'envol et ces jeunes avaient une masse corporelle moindre que ceux dans l'aire non brûlée, peut être parce qu'il y avait moins de proies disponibles immédiatement après le feu. Il est néanmoins remarquable que des oiseaux aient poursuivi leur reproduction compte tenu de la profonde altération de l'habitat causée par le feu. L'occupation du territoire en 2003 était semblable à 1995, l'année du feu, dans l'aire brûlée mais avait diminuée dans l'aire non brûlée. Il semble donc que l'aire non brûlée devient un habitat de moins en moins adapté à mesure que la forêt prend de la maturité alors que l'aire brûlée demeure un habitat viable pour les crécerelles. Nous présentons ici des évidences qui suggèrent que les différences d'occupation entre les aires brûlée et non brûlée pourraient être dues à une quantité moindre de prédateurs de nids dans l'aire brûlée en 2003.

Mots-clés: abundance de proies, crécerelle d'Amérique, Falco sparverius, feux de forêt, forêt boréale, occupation du territoire, succès reproducteur.


Introduction

The boreal forest is a fire-driven ecosystem. At infrequent intervals, often on the order of 100 y, weather conditions are favourable for large-scale, high-intensity fires that spread rapidly and cause major changes in vegetative cover (Johnson, 1992). The behaviour of these stand-replacing fires does not appear to be affected by areas having previously been burned by smaller fires of lower intensity; as a consequence, much of the variation in landscape and habitat configuration of the boreal forest has been determined by large-scale fire events (Rowe, 1972; Johnson, 1992).
Wildlife that inhabit boreal regions are expected to be adapted to these disturbances, given the repetitive nature of stand-replacement fires (Hunter, 1993).

Many areas of the boreal forest, such as the southern mixedwood region of western North America, have come under intense harvesting pressures (Cumming et al., 1994), and there is presently concern over the ecological effects of such activities. Concomitantly, there is also much interest in having harvesting activities mimic natural disturbance regimes such as forest fires and subsequently documenting how diversity and richness of wildlife species varies between harvested and burned forests (Simon, Schwab & Otto, 2002). Many studies have focussed on abundance of birds and have shown that certain species are more prevalent in recently burned landscapes than either harvested blocks or mature forest (Hutto, 1995; Hobson & Schieck, 1999; Simon, Schwab & Otto, 2002; Hannah & Hoyt, 2004). Although most studies have used census techniques to determine population estimates, some also have been able to compare how reproductive success of birds varies between burned and unburned sites, using both cross-section studies (Saab & Vierling, 2001) and longitudinal data (Dawson & Bortolotti, 1999). Nonetheless, despite increasing knowledge of the role of fire in the ecology of avian species, little information exists on the proximate responses of individual birds to fire in the boreal forest, such as how reproduction is impacted by fire sweeping through their territories during the breeding season.

We have shown previously that reproductive success of the American kestrel (*Falco sparverius*), a small falcon, in the year following a large forest fire in the boreal forest of Saskatchewan was not significantly impacted compared to birds occupying an adjacent unburned control area (Dawson & Bortolotti, 1999). We hypothesized, and confirmed with empirical data, that adequate food resources in the burned area allowed birds to breed successfully. Here, we extend these previous observations and examine the immediate effect of a large forest fire, and its profound alteration of habitat, on kestrels during a single breeding season. In addition, we also examine territory occupancy by kestrels in the burned and control areas 8 y following the fire. In the mixedwood boreal forest of Alberta, Hobson and Schieck (1999) showed that while kestrels were more likely to be found in burned as opposed to harvested areas, they were most abundant in the year immediately following a fire. In contrast, Hutto (1995) could detect no effect of time since burning on abundance of kestrels in coniferous forests of the Rocky Mountains, Montana. Therefore, a secondary goal was to investigate whether changes in occupancy occurred in the burned area versus the control area after 8 y.

**Methods**

**Study area**

We studied American kestrels in the boreal forest of north-central Saskatchewan, Canada, in the area around Besnard Lake (55° N, 106° W). The study area is at the southern edge of the Precambrian Shield and is at the transition of the northern coniferous and mixedwood sections of the boreal forest region (Rowe, 1972). Jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and black spruce (*P. mariana*) are the dominant tree species, growing both in mixed and pure stands. From the mid-1970s to the mid-1980s, much of the mature jack pine in the area was harvested for pulp. Limited harvesting, particularly of trembling aspen, continues to occur in the area. Gerrard, Bortolotti, and Wiebe (1996) provide detailed descriptions of the physical and ecological attributes of the area.

**Field work and forest fire: 1995**

Kestrels arrive in our study area in mid to late-April, and most clutches are initiated in mid to late-May. At the beginning of the 1995 field season, there were 371 nest boxes available for breeding along roadways and logging trails. Boxes had several centimetres of clean wood shavings in the bottom and were mounted about 4 m above the ground on trees in a variety of habitats ranging from open clearcuts to forested roadsides. Previous research in our study area has shown that natural cavities are ubiquitous and providing nest boxes does not appear to influence population densities of kestrels (Bortolotti, 1994). Each nest box was visited every 3 to 5 d from mid-May to mid-June, or until egg laying had started. We returned when laying was complete to ascertain clutch size and capture adults. Each adult bird was banded, weighed to the nearest gram, and six measures of size were taken: length of the unflattened wing chord, central rectrix, outer rectrix, and tenth primary flight feather (nearest mm); length of the exposed culmen; and width of the tarsus (nearest 0.1 mm). We obtained an index of body size using the first component of a principal components analysis (PCA). The six linear measurements were used as input variables for the PCA, and we performed separate analyses for females (*n* = 97) and males (*n* = 83). Mass of an animal is partly a function of its structural size, so to obtain an index of body condition we removed the effect of body size by regressing mass against PC1 separately for each sex (females: *F*₁,₉₅ = 6.79, *P* = 0.01; males: *F*₁,₈₃ = 3.58, *P* = 0.06) and used the residuals as our measure of condition. Only those birds captured after the fire had started (see below) are included in analyses.

We visited nests again to determine hatching date and the number of eggs that had hatched. Nests were then monitored periodically throughout the brood-rearing period. As measures of offspring quality, we weighed each nestling (nearest g) and measured their tenth primary flight feather (nearest mm) when they were 24 d old, just prior to fledging. Number of young fledged was determined by visiting nests after fledging and subtracting the number of dead chicks found in nests from brood size at 24 d. We were unable to collect all of these data for a number of nests in the burned area because authorities restricted our access to parts of the area when the fire was actively burning, and some nests were consumed by the fire (see below).

A lightning strike ignited a wildfire on 28 May 1995. The fire burned until it was extinguished by heavy rains on 10 July 1995. The western portion of our study area was consumed, and the total area of the burn was approximately 72,000 ha (Saskatchewan Forest Fire Management Branch, pers. comm.; see Figure 1 in Dawson & Bortolotti, 1999).
We had 64 nest boxes in the burned area before the fire, and 19 of the boxes (eight occupied by kestrels) were consumed in the fire. As the fire occurred in the middle of the breeding season for our kestrels, this allowed us to compare subsequent reproductive performance of kestrels in the remaining occupied nest boxes in the burned area to a group of control nests in the adjacent unburned area. For this control group, we included only those nests that were not manipulated as part of our other research. The majority of such nests were manipulated after hatching (Dawson & Bortolotti, 2002; 2003), and so data from these nests were included in analysis of hatching success and number hatched, but not in tests of the effect of the burn on fledging success or offspring performance.

FIELD WORK: 2003-2004

In the spring of 1996, we replaced the 19 nest boxes that were destroyed in the fire with new ones. Replacement boxes were erected at the same location and, in nearly all cases, in the same tree (Dawson & Bortolotti, 1999). We continued to study kestrels intensively in the Besnard Lake area until 1997. Between 1998 and 2002, none of the nest boxes were monitored. In April 2003, many of the original nest boxes were repaired or replaced as necessary (same tree whenever possible), although some nest box locations were no longer accessible because logging trails had deteriorated. We checked some boxes later in the season for occupancy by kestrels, but most boxes were not visited again until April 2004. We were able to reliably determine occupancy by kestrels by the presence of feces and prey remains, or egg shells in the case of depredated nests. The majority of nest losses incurred by kestrels in our study area were due to predation by red squirrels (Tamiasciurus hudsonicus; R. D. Dawson & G. R. Bortolotti, unpubl. data), so we also noted whether there was evidence of occupancy by squirrels, including grass nests and feces. Occupancy by kestrels and squirrels was determined for 159 control boxes and 32 boxes in the burned area.

DATA ANALYSIS

We recognize that our study is replicated and any differences that we detect could be due to the effects of the fire, or because of inherent differences between the burned and control areas. However, a previous study showed that prior to the fire, there were no significant differences between the burned and control areas in nest box occupancy, clutch initiation dates, clutch and egg size, brood size at fledging, or mass and length of tenth primary of offspring at fledging (Dawson & Bortolotti, 1999). Therefore, the two areas were comparable.

For data collected during the year of the fire, analysis of variance was used to test whether body condition of parent kestrels differed between the burned and control areas. We used $G$ tests and Fisher’s exact tests to determine whether there were differences between the burned and control areas in the proportion of nests hatching at least one egg and fledging at least one chick. For nests where at least one egg hatched, we calculated the proportion of eggs that successfully hatched, as well as the proportion of hatched eggs that successfully produced fledged young. We then tested whether there were differences in these two variables between the burned and control areas using Mann-Whitney $U$ tests.

To examine the effects of the fire on offspring mass and primary length at 24 d of age, we analyzed data separately for male and female offspring because the species show sexual size dimorphism in the nest (Dawson & Bortolotti, 2000). To avoid pseudoreplication, we calculated mean mass and primary length per nest for each sex. We were unable to access some of the nests in the burned area until the fire was contained, and so we lack accurate hatching dates, and therefore age of offspring, for some nests. These nests were not included in analyses of offspring mass and primary length, and so sample sizes differ from analyses of hatching and fledging success. For each variable, we first used analysis of covariance with area as a main effect and brood size at age 24 d as a covariate, plus the interaction between area and brood size. We then tested three other models where the interactions, followed by either area or brood size, were sequentially excluded. Next, we used Akaike’s Information Criterion (AIC) corrected for small sample size (AICc), along with model weights and evidence ratios (details in Burnham & Anderson, 2002), to choose which of the four candidate models best described the data for each variable.

To test whether nest box occupancy had changed in the burned and control areas between 1995 and 2003, we used data from all boxes that were present and useable in both years. As occupancy of individual boxes in 1995 and 2003 were not independent observations, we used McNemar change tests for paired observations (years as matched pair) to examine whether occupancy changed in both the control area and the burned area. Data were analyzed using SPSS (Norusis, 2000). Means are presented ± 1 SE, and results were considered significant at the 0.05 level.

Results

The fire in our study area in 1995 began burning at the time of the breeding season when most American kestrels had finished egg laying and were in the early stages of incubation. In general, the incubation period coincided with the period during which the fire was actively burning, and so kestrels raised their offspring after the fire. As is typical of fires in the boreal forest (Johnson, 1992), even if some small patches remained partly unburned, a considerable area was exposed to a hot fire and most trees were killed but remained standing. Although 45 of 64 nest boxes survived the fire, the areas surrounding each of these nest boxes was burned, and nearly every tree that had a nest box was killed by the heat of the fire. Also, during the course of the fire, and in particular the first two weeks, the area was blanketed in thick smoke that reduced visibility to less than a few metres on some days. Overall, the habitat in the burned area was extraordinarily altered by the fire.

We excluded the eight nest boxes occupied by kestrels that were destroyed by the fire from the analyses of 1995 data. There was no difference in body condition between the burned and control area for either female ($F_{1, 95} = 1.1, P = 0.3$) or male ($F_{1, 81} = 1.8, P = 0.2$) parents during incubation (all birds captured after the start of the fire). Overall, we found
no effect of the fire on the ability of kestrels to hatch at least one egg ($G = 0.3$, df = 1, $P = 0.6$), with 76% (16/21) of occupied nests in the burned area hatching young, while 71% (53/75) of occupied control boxes had successful hatching. Among boxes where at least one egg hatched, the proportion of eggs hatching did not differ between burned and control areas ($U = 310.0$, $Z = -0.4$, $P = 0.7$; Figure 1a). Complete failure during the brood-rearing period was rare (1/16 burned nests, 3/53 control nests), and there was no difference between control and burned areas in the proportion of nests fledging young (Fisher's exact test, $P = 1.00$). The proportion of young successfully fledging in each nest was significantly higher in the control area than in the burned area ($U = 256.5$, $Z = -2.1$, $P = 0.04$; Figure 1b).

Overall, we collected data on mass of male nestlings from 43 control and 10 burned nests and for females from 40 and 10 nests, respectively (difference in sample sizes is due to three nests containing only male nestlings). Sample sizes for length of tenth primary were similar except that we collected data from only eight burned nests because fire crews did not allow free access to the burned area and so we only had sufficient time to weigh chicks at some nests.

For mass of female offspring at 24 d, the best model suggested by AICc to explain the data included both area and brood size as predictor variables. This model showed that mass of female nestlings declined significantly as brood size increased ($F_{1, 47} = 9.4$, $P < 0.01$), and mass was higher in the control area than in the burned area ($F_{1, 47} = 10.5$, $P < 0.01$; Figure 2a). For mass of male offspring, AICc indicated that the model with brood size ($F_{1, 51} = 15.4$, $P < 0.001$) fit the data equally well as the model containing both area and brood size effects ($\Delta$AICc $< 1$). The results from the latter model showed that mass of male nestlings declined significantly as brood size increased ($F_{1, 50} = 17.7$, $P < 0.001$), and there was a non-significant trend for mass to be higher in the control area than in the burned area ($F_{1, 50} = 3.8$, $P = 0.06$; Figure 2b). It appeared that the fire did not influence the length of tenth primary of female offspring, as AICc indicated that the model including only brood size ($F_{1, 46} = 7.3$, $P = 0.01$) best fit the data. For male offspring, AICc was unable to distinguish between a model with only brood size and one with only area ($\Delta$AICc $< 1$). Nonetheless, these models fit the data poorly as neither analysis was significant (brood size model: $F_{1, 49} = 0.1$, $P = 0.8$; area model: $F_{1, 49} = 0.2$, $P = 0.7$), suggesting that other factors not considered in this study were driving variation in feather length.

In the control area, 73 of 159 boxes were occupied by kestrels in 1995, whereas only 49 of these boxes were occupied in 2003 (McNemar change test, $P < 0.01$). In contrast, occupancy of individual nest boxes did not vary between 1995 and 2003 in the burned area ($P = 0.4$), with 10 of 32 and 14 of 32 occupied in 1995 and 2003, respectively (Figure 3). Occupancy of nest boxes by red squirrels increased between 1995 and 2003 in both the control (1995: 32/159; 2003: 73/159; $P < 0.001$) and burned areas (1995: 4/32; 2003: 10/32; $P = 0.07$), but the results were only significant for the control area.
Discussion

American kestrels breeding in the boreal forest in the portion of our study area that burned were just as likely as birds in the control area to hatch at least one egg, and to hatch similar numbers of eggs (Figure 1). These results suggest that the fire itself, as well as the profound change in habitat, did not hamper the ability of kestrels to successfully incubate their eggs. These results are somewhat surprising, because while kestrels are known to be fairly resilient to disturbance, the degree of disruption that they encountered in the burned area during the fire was much higher than in a normal breeding season. Apart from researchers, encountering humans in the study area was probably a relatively rare occurrence for most of our birds; however, during the fire there were large crews of firefighters in the area, fixed-winged aircraft frequently dropped water on the actively burning fire, and there were no fewer than 12 jet turbine helicopters transporting fire crews and bucketing water on the fire. But, a potentially more significant factor disrupting parental behaviour was smoke. For several weeks during the incubation period, visibility was often limited to only a few metres or less. How kestrels could even navigate to return to the nest after foraging during an incubation recess is a mystery. In addition, at least for humans, the thick smoke was noxious and made breathing difficult. Despite this, we also were unable to detect any detrimental effects of the fire on the body condition of parent kestrels during the incubation period.

Similar to our results for hatching success, we could not detect an immediate effect of the fire on whether or not a pair was able to successfully fledge at least one offspring. Birds breeding in the burned area did, however, fledge fewer offspring than pairs in the adjacent control area (Figure 1). In addition, mass of female nestlings just prior to fledging was significantly lower in nests from the burned than from the control area, and a similar but non-significant difference was also detected for male nestlings (Figure 2). While disturbance may be the underlying cause of the reduced number of young fledged, as well as the reduced mass of offspring at fledging, we believe that this was the consequence of immediate reductions of food abundance during and immediately after the fire. In our study area, the main prey of kestrels is red-backed voles (*Clethrionomys gapperi*; Bortolotti *et al.*, 2000). These voles are usually thought to be associated with late successional forests, and their numbers are known to be severely reduced immediately following forest fires (Simon *et al.*, 1998; Simon *et al.*, 2002; Nappi, Drapeau & Savard, 2004). This may also have forced birds to fly long distances to unburned areas to forage. Lack of adequate food supplies may therefore account for the reduced number of nestlings surviving to fledging, and the lower body mass of those that did survive, in burned nests.

Food availability is an important component of reproductive success of kestrels in our study area (Dawson & Bortolotti, 2000; 2002), and hatching asynchrony, brood reduction, and sex ratio manipulation have all been related to variation in numbers of small mammals (Bortolotti, Wiebe & Iko, 1991; Wiebe & Bortolotti, 1992; 1994). Our results showing that the fire did not affect parental condition but did have detrimental effects on number and mass of offspring are consistent with our previous studies. Parental investment decisions of American kestrels appear to be geared towards favouring their own survival as opposed to their offspring. For example, we have shown that when food was supplemented to nests during brood rearing, female parents responded by reducing their rates of provisioning and consuming much of the extra food, which resulted in them having enhanced survival rates (Dawson & Bortolotti, 2002). Similarly, experimental reductions in brood size caused male parents to reduce their rates of per-capita food delivery (Dawson & Bortolotti, 2003). Presumably under conditions of food shortage, such as may have occurred in the burned area, their reactions would have been to ensure their own well-being as opposed to that of their offspring. If the fire did in fact reduce food availability in the present study, it also appears that the consequences were more severe for female than male offspring (Figure 2). American kestrels show sexual size dimorphism while still in the nest, with females being larger than males (Dawson & Bortolotti, 2000), so food requirements of female offspring are higher than those of males (Anderson *et al.*, 1993). Wiebe and Bortolotti (1992) have shown that during periods of food shortage, parent kestrels are more likely to bias their broods
in favour of the smaller sex. Our results showing that mass of female offspring in the burned area at fledging was reduced to a greater extent than that of males provide additional support for reductions in food having greater impacts on female offspring (Figure 2).

We showed previously that there were no differences between the burned and control areas with respect to numbers of small mammals in the year following the fire (Dawson & Bortolotti, 1999). These results were surprising because populations of red-backed voles are thought to be reduced immediately after a fire and only begin to increase as regeneration proceeds and shrub cover increases (Simon et al., 2002; Nappi, Drapeau & Savard, 2004). In North America, however, numbers of deer mice (Peromyscus maniculatus) increase dramatically soon after a forest fire (Gliwicz & Glowacka, 2000), presumably in response to increased seed abundance that results from heating of serotinous and semi-serotinous cones of some species of coniferous trees (Johnson, 1992). Although we had analyzed data for abundance of all types of small mammals in our original study (Dawson & Bortolotti, 1999), further examination of our data set revealed that numbers of deer mice did not differ between the burned and control areas in the year following the fire (F1, 42 = 1.5, P = 0.5; R. D. Dawson & G. R. Bortolotti, unpubl. results). Sufficient food for kestrels appeared to be available in the year following the fire (Dawson & Bortolotti, 1999), but we believe that a lack of food during the year of the fire is an adequate explanation for the reduced success of kestrels in the burned area during the year of the fire (Figures 1 and 2).

Overall, the fact that any of the kestrels remained in the burned area during and immediately following the fire is remarkable. In many cases, the landscape for kilometres surrounding a nest box was completely blackened, with no green plants visible. The adult birds that we captured in the area, as well as nestlings, were usually completely covered with soot. However, only two nests in the burned area were abandoned by parents during the fire, so as a general rule, if the nest box was not completely consumed by the fire, the birds remained to continue their nesting attempt. Kestrels in our study area eat a variety of insects, amphibians, and birds in addition to small mammals (Bortolotti et al., 2000; R. D. Dawson, unpubl. data). Although numbers of small mammals may have decreased immediately following the fire, some insects such as boring beetles probably increased (see review in Nappi, Drapeau & Savard, 2004), so the generalist nature of kestrels and their ability to shift to different types of prey may be a contributing factor in their resilience to the face of phenomenal habitat changes and potentially large reductions in their main prey.

Some species of birds may be reliant on recently burned areas for continued viability of their populations (see Hutto, 1995), while others are known to at least prefer such areas (Hobson & Schieck, 1999; Hannah & Hoyt, 2004). For example, northern hawk-owls (Surnia ulula) are often found in recently burned areas (Dawson & Bortolotti, 1999), presumably because of increased prey abundance and ease of hunting (Hannah & Hoyt, 2004). But, these owls are rarely seen in burned areas older than 8 y, or in mature forests (Hannah & Hoyt, 2004). As habitats may become less suitable for birds of prey as burned areas regenerate, we were therefore interested in determining whether changes in territory occupancy occurred in the burned area 8 y after the fire. This was not the case, as occupancy of nest boxes remained the same in the burned area, but declined in the control area (Figure 3). The habitat in the control area has continued to age since 1995 and is perhaps becoming unsuitable.

Occupation frequency of a territory is often considered to be a surrogate of habitat quality (Sergio & Newton, 2003), so this suggests that the burned area is still a viable habitat for generalist predators such as kestrels. In addition to immediate reductions in numbers of voles and mice, it is thought that populations of nest predators are lowered by forest fires (Saab & Vierling, 2001; Saab, Dudley & Thompson, 2004). Our results may be partially driven by predation, because while occupancy of nest boxes by red squirrels increased in both the burned and control areas between 1995 and 2003, the increases were most pronounced in the control area (Figure 3). We should, however, expect that predation risk will increase with the age of the burn, as the area continues to be re-colonized by predators such as red squirrels from surrounding unburned areas. Further research will be required to address this issue, and more importantly, to determine whether reproductive success of kestrels in the burned area has changed through time.

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