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Short communication

Capercaillie *Tetrao urogallus* nest loss and attendance at Abernethy Forest, Scotland

Ron W. Summers, Johanna Willi & Jennifer Selvidge

Improvement of breeding success is key to capercaillie *Tetrao urogallus* conservation in Scotland. However, factors affecting breeding success are not fully understood, including the cause of nest loss. We monitored 20 capercaillie nests with video or digital cameras at Abernethy Forest, Scotland to measure nest loss, determine causes of losses, and describe nest attendance by females. The mean date for the onset of incubation was 15 May and mean clutch size was 7.25 eggs. During incubation, females usually left the nest twice a day (range: 0-4), on average 28 minutes after sunrise and 2 hours 13 minutes before sunset, for a total of 53 minutes per day. There were no egg losses during egg laying, and the daily loss of clutches during incubation (26 days) was 0.0427 (95% CI = 0.0191-0.0663). However, an experiment with artificial nests suggested that predation rates were higher where video cameras were installed than at nests where they were not. After adjusting for the potential effect of deployment of the video system, the daily loss of the capercaillie nests was 0.0205 (95% CI = 0.0074-0.0554). Thus, the probability of a nest failing was 0.68 (95% CI = 0.39-0.83, unadjusted) or 0.42 (95% CI = 0.18-0.77, adjusted). This adjusted estimate at Abernethy Forest was close to the mid-range of other studies of capercaillie nest loss in Scotland and elsewhere in Europe. Eleven of the nests were depredated, nine by pine martens *Martes martes* and two by unknown predators. One nest was abandoned. Based upon unadjusted daily predation rates, predators destroyed 65% of nests (57% known to be by pine martens) or, after adjusting for the potential effect of the video system, 39% of nests (33% known to be by pine martens). A better understanding of factors affecting pine marten (a protected species in the UK) numbers and hunting patterns is required before a habitat management plan can be implemented to reduce pine marten predation on capercaillie nests.

Key words: capercaillie, nest loss, nest attendance, pine marten, predation, Scotland, Tetrao urogallus, video camera

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For many birds, predation is the main cause of loss of eggs and chicks (Lack 1954, Newton 1998) and can significantly reduce breeding success, especially in ground-nesting birds (Côté & Sutherland 1997). The breeding success of grouse is strongly affected by predators (Angelstam et al. 1984), as shown by both correlative (Kurki et al. 1997) and experimental studies in Fennoscandia (Marcström et al. 1988, Kauhala et al. 2000). Red fox *Vulpes vulpes* and pine marten *Martes martes* appear to be the main predators in Fennoscandia, but the relative importance of each is often not determined (Marcström et al. 1988, Kurki et al. 1997, Kauhala et al. 2000). The identification of nest or chick predators

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usually requires a specialised study (Wegge & Kastdalen 2007).

Capercaillie *Tetrao urogallus* numbers in Scotland have declined since the 1970s (Moss 1994) and the last population estimate was 1,980 birds (95% CI = 1,284-2,758) in winter 2003/04 (Eaton et al. 2007). The decline has been attributed to fully-grown birds colliding with forest fences (Baines & Summers 1997, Moss et al. 2000) and poor breeding success that was correlated with an index of temperature change in April, frequent rainfall in June, and high predator abundance (Moss 1986, Moss et al. 2001, Baines et al. 2004). Mortality due to fences has been reduced by removing or marking fences (Baines & Andrew 2003), but attempts to improve breeding success has proved less tractable.

In an earlier 11-year study from 1989 to 1999 at Abernethy Forest, breeding success was best in years with little rainfall in June and when indices of predator activity were low (Summers et al. 2004). In that study, crows *Corvus corone* and *C. cornix* were identified as key predators, although breeding success was also negatively related to the combined activity of crows and mammalian predators. The latter could not be specifically identified but could have included red foxes, pine martens and possibly badgers *Meles meles*. During the 11-year study at Abernethy, pine martens became more abundant, and the index of activity of mammalian predators, as measured by losses of artificial clutches, rose over the last four years of the study (Summers et al. 2004). In addition, automatic cameras recorded pine martens depredating artificial clutches. However, in a study of 14 forests (including Abernethy Forest) in Scotland in 1995, the absence of a significant correlation between breeding success of capercaillie and an index of pine marten abundance suggested that the pine marten was probably not a major predator (Baines et al. 2004). Nevertheless, studies in Fennoscandia strongly implicate the pine marten is a predator that can help depress the breeding success of woodland grouse (Marcström et al. 1988, Kurki et al. 1997, Kauhala et al. 2000).

Despite ongoing successful control of crows and partial control of red foxes at Abernethy Forest, the breeding success of capercaillie exceeded one chick per female only once during 2000-2007. Therefore, further work was required to address the low productivity. In particular, there was a lack of empirical data on capercaillie nest loss and the predator species involved. Therefore, to provide data on the relative effect of different nest predators on the hatching success of capercaillie, we studied nest loss, the causes of nest losses, and we described nest attendance to establish whether predation was associated with the time of arrival of the female at the nest after her short absences each day.

Methods

Study area

Our study was carried out at Abernethy Forest (57°10'N, 3°40'W), a 36 km^2 pinewood on the northern slopes of the Cairngorm Mountains in the central Highlands of Scotland. The forest largely comprises semi-natural Scots pine *Pinus sylvestris* woodland and pine plantations (Summers et al. 1997). Abernethy Forest is one of about 80 woods containing semi-natural Scots pinewood in Scotland (Mason et al. 2004), several of which have capercaillie densities higher than in conifer plantations (Catt et al. 1998). Semi-natural pinewoods are descended from one generation to the next by natural means, but have been exploited by man for hundreds of years (Steven & Carlisle 1959). This is in contrast to present-natural woodland, the state which would prevail if humans had not been a significant ecological factor (Peterken 1996). The plantation stands at Abernethy were at the following stages of development: stand initiation, stem exclusion and understorey reinitiation (Oliver & Larson 1996), and the median ages of the pines in different stand types ranged from 11 to 67 years. The semi-natural woodland was at understorey reinitiation and old-growth stages and the median ages in different stand types ranged from 67 to 149 years (Summers et al. 2008). Control of crows and red foxes was carried out each spring and summer during the study. Therefore, few crows bred and most young red foxes were culled, but the number of adult foxes was less affected (Summers et al. 2004). Pine martens have been legally protected in Britain since 1988, when added to Schedule 5 of the Wildlife and Countryside Act 1981 (Birks 2002), so this species was not controlled.

Nest searching and nest loss

We searched for nests in May during 2003-2007, mainly in arbitrarily chosen patches of semi-natural pinewood close to vehicular gravel tracks to allow easy transportation of equipment to nest sites, though we also searched elsewhere. To test the

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possibility that searches close to tracks led to a disproportionate number of nests being found close to tracks, we compared the distance to the nearest track for the capercaillie nests with the distance to the nearest track for a series of systematic points across the forest. The intersections of 1-km national grid lines were chosen as the systematic points.

Searches were carried out by groups of up to 20 staff from the Royal Society for the Protection of Birds and volunteers walking abreast spaced at 2-m intervals. Searches were also carried out by two people using a 7-m long drag rope, with plastic rattles at 1-m intervals. Each year, we searched an average of 155 ha (range: 91-266 ha) of woodland, and spent 899 man-hours to find 18 nests (50 man-hours per nest). Two other nests were found by chance during other work. When a female was flushed from its nest, video surveillance equipment was installed (see below), and that nest was not revisited until the clutch hatched or was depredated. The daily rate of nest loss was determined from the number of lost nests divided by the cumulative number of days of observation for all nests (Mayfield 1975). Standard errors were obtained from Johnson's (1979) equation. Nest survival during incubation was calculated by raising the daily survival rate (1 - rate of loss) to the power of 26, the length of the incubation period in days (Storch 2001). By applying the Mayfield method, we assumed that the daily predation rate was constant during incubation. However, the laying period, over which eggs were laid during short visits to the nest at two-day intervals, was treated separately because predators may have different cues associated with finding nests at this stage of nesting.

The video system

A time-lapse video or digital (for the last three nests) recording system was installed at the capercaillie nests. The video system consisted of a camera mounted on a camouflaged (with brown and green paint, and heather *Calluna vulgaris* sprigs) stick 2 cm thick, connected by a 30-40 m cable to a video recorder in a weatherproof case. The lens (5 mm in diameter) was placed 30-100 cm from the nest to give an overhead or side view of the female, and of her clutch when she left the nest. Infrared diodes around the lens provided night-time viewing. A 12-volt lead-acid 'cyclic' battery powered each video system. A 3-hour video cassette lasted more than 24 hours while recording an image every fifth of a second. The battery and cassette were replaced daily, without flushing the female. Occasionally, at weekends, we used two batteries in parallel and a 5-hour cassette gave a recording time of 48 hours. The digital system installed at three nests recorded only movements on and off the nests, and stored images from several days (Bolton et al. 2007).

The following information was retrieved from the tapes or digital cards: times of arrival and departure of the female from the nest, number of eggs when the female departed, hatching of chicks and details of any predation event. ANOVAs were used to test for differences in the number and times of departure amongst females. After the camera deployment, vegetation partially obscured the lens at two nests, making detailed descriptions of events difficult. All times refer to Greenwich Mean Time.

Did the video equipment affect the predation rate?

It was possible that the video equipment attracted predators, as has been shown for markers close to nests (Picozzi 1975, Hein & Hein 1996). Mammalian predators may have followed rather than crossed the cable between the camera and video recorder, either because the animal was inquisitive, or reluctant to cross it. However, it is also possible that predators may have shied away from a strange structure in the forest (Hernandez et al. 1997, Herranz et al. 2002). To test whether the video system affected the predation rate of nests and hence biased the results, we compared survival of artificial nests (a group of five or six domestic hen's eggs) with a simulated video system ($N=46$) and without the system ($N=46$). The simulated system was a camouflaged stick with a 30-40 m rope leading to a black plastic bag pinned to the ground. The artificial nests were set out in the areas that were searched for capercaillie nests. Forty-six pairs were deployed over three years between 30 April and 20 June, with the nests in each pair about 50 m apart in the same type of woodland. They were checked weekly for four weeks. Daily loss rates were calculated for each group (Mayfield 1975) and standard errors obtained using Johnson's (1979) equation. To compare loss of 'video' and control nests, we employed a Generalised Linear Model in which a binary nest outcome (depredated or survived) was modelled, with number of exposure days as the denominator to derive rate of loss. A logit link function was applied (Crawley 1993) and the analysis carried out in SAS (SAS Inst. 2000).

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Results

Egg laying, incubation and hatching

Among the 20 nests that we found, 14 contained complete clutches, but in six nests, egg laying was incomplete. For the nests with complete clutches, the females took, on average, 2 hours 55 minutes (range: 33 minutes - 6 hours 48 minutes) to return to the nest after deployment of the camera. In contrast, the time for females to return to incomplete egg sets to lay the next egg was 31 hours (range: 16-50 hours).

During egg laying, females usually made a single visit to the nest between 06:00 and 17:00 hours every second day to lay an egg. Visits lasted about 2 hours on average (range: 1 hour 14 minutes - 5 hours 20 minutes). After an egg was laid, the female started her departure by picking up small pieces of loose vegetation in front of the nest and tossing them over her back to the left and right. This procedure continued as she stood up and walked slowly from the nest, resulting in partially covered eggs.

During incubation, the females usually left the nest twice a day (mean = 2.0, SD = 0.2, N = 16 females), in the early morning and evening (Fig. 1), without covering the eggs. There were significant differences among females in the number of departures ($F_{15, 180} = 2.15$, $P = 0.009$). For those days on which there was more than one absence, the morning departure took place, on average, 28 minutes after sunrise (SD = 68 minutes) for 16 females and the absence lasted 24 minutes (SD = 5). On average, the evening departure took place two hours and thirteen minutes before sunset (SD = 80) and lasted 28 minutes (SD = 3). Total absence per day was 53 minutes, on average (SD = 10). There were significant differences among females in the total absence time ($F_{15, 178} = 2.54$, $P = 0.002$), but no difference between the duration of first and last departure periods ($F_{1, 304} = 1.93$, $P = 0.17$), although there was a significant interaction ($F_{16, 304} = 3.34$, $P < 0.001$), showing that some females had longer morning departures than evening ones, whilst others had longer evening departures.

The mean clutch size was 7.25 eggs (SD = 1.1, range: 6-10, N = 20). The mean date for the onset of incubation, using either observed laying dates (N = 6), or subtracting 26 days from the observed hatching (N = 6), was 15 May (range: 3 - 30 May, N = 12). This may have included second layings after loss of a first clutch. Partial loss of the clutch occurred at two nests. In both cases, the female appeared to have knocked an egg out of the nest during a departure. Of those nests that were not depredated or abandoned, 53 chicks hatched from 61 eggs (hatchability of 86.9%), and the mean brood size at hatching was 6.6 (SD = 1.8).

Nest locations in relation to tracks

The median distance of capercaillie nests from the nearest vehicular gravel track was 65 m (N = 20, range: 6.5-495 m). For comparison, the median distance of 37 systematic points to the nearest track was 100 m (range: 2-1,018 m). There was no significant difference between the two values (Mann-Whitney U = 374.5, P = 0.69). Therefore, nest searching did not lead us to find a disproportionate number of nests close to tracks.

Did the video system affect the predation rate?

Sixteen of the 46 artificial nests with a simulated video system were depredated and eight of the 46 control nests were depredated. The respective daily predation rates of artificial nests with a simulated video system and control nests were 0.0154 (SE = 0.0038) and 0.0073 (SE = 0.0026), indicating the nests with 'video' systems were 0.0154/0.0073 = 2.11 times more likely to be depredated. However, this

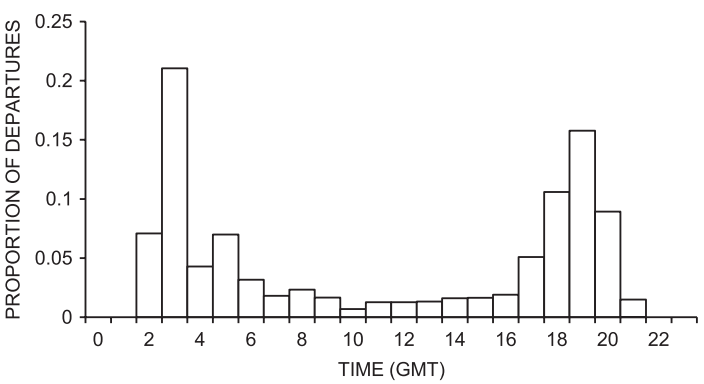


Figure 1. Times of departures by 11 female capercaillie from their nests. Values for each female were weighted to account for the differing number of records for each female.

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difference was not statistically significant as a two-tailed test ($\chi^2 = 2.44$, $P = 0.12$), but almost so as a one-tailed test ($P = 0.06$), if one accepted that the video system was likely to attract predators. Therefore, to allow for the possibility that the video system did attract predators, we calculated an adjusted daily rate of loss of natural nests. This was done by adding the estimate for the effect of the artificial nests in the logistic equation describing the rate of daily failure.

Loss among capercaillie nests

There were no losses during the 38 days of observation at the six capercaillie nests during egg laying. However, out of the 281 days of observation at the capercaillie nests (N = 20) during incubation, there were 12 losses, 11 due to predation and one due to desertion. Therefore, the daily loss rate was 0.0427 (SE = 0.0121); 0.0391 to predation (SE = 0.0116). However, adjusting these losses to account for the possible increase in likelihood of predation due to the presence of the video equipment, the estimated daily loss rate of nests without video equipment was 0.0205 (95% CI = 0.0074-0.0554). Given an incubation period of 26 days, the probability of a nest failing to hatch was 0.678 (95% CI = 0.394-0.832, unadjusted) or 0.416 (95% CI = 0.176-0.773, adjusted).

The only predator identified was the pine marten (at nine nests). The abandoned clutch was also taken by a pine marten, 12 days after the desertion. Condensation on the lens after rainfall meant that predator identification was not possible at the other two depredated nests. Both nests were cleared of eggs, and at one nest, a scattering of 52 capercaillie body feathers lying within 2 m of the nest suggested that a predator had attempted to catch the female. Among only the nests with incubating females, the unadjusted daily predation rate by predators was 0.0391 (95% CI = 0.0165-0.0618) for all predators and 0.0320 (95% CI = 0.0114-0.0526) for pine martens. The respective adjusted values were 0.0187 (95% CI = 0.0073-0.0561) for all predators, whilst the predation rate by pine martens was 0.0153 (95% CI = 0.0071-0.0580). Therefore, the unadjusted probability that a capercaillie clutch was taken by a predator was 0.646 (95% CI = 0.351-0.810) and specifically by a pine marten was 0.571 (95% CI = 0.259-0.757). The adjusted probability that a capercaillie nest was taken by a predator was 0.388 (95% CI = 0.173-0.777), and that it was taken by a pine marten was 0.330 (95% CI = 0.168-0.788).

Pine martens arrived, on average, 8 hours 46 minutes (range: 2 hours 33 minutes - 18 hours 50 minutes) after the last arrival of the female. Therefore, there was no evidence that pine martens followed capercaillie females when they returned to their nests, although most times of arrival by females at the nests did occur close to dawn and in the evening when pine martens were active (see Fig. 1). Predation by pine martens occurred between 20:22 and 04:43 hours, and at all nests, the female departed within a few seconds before the pine marten appeared. At one nest, the pine marten leapt across the nest, clearly attempting to catch the departing female. However, there was no evidence that the female was caught. At eight nests where all details could be observed, the pine martens removed the eggs one at a time in their mouths. The average interval between visits was 5.2 minutes (N = 8 nests), and at all nests, the pine marten returned to the empty nest for at least one further inspection. We found no eggs or shells when we later searched a 50-m radius of the nests. The average time to clear the nests of eggs and return for a final visit(s) was 36 minutes. Five of eight female capercaillie returned to their empty nests 46 minutes (range: 7 minutes - 2 hours 2 minutes) after the last visit by the pine marten. They spent 2-13 minutes at the nest, occasionally shuffling down in the empty scrape and pecking at the surrounding vegetation before departing.

At one nest, the predation event was different from those described above. The pine marten took the first egg and, while still at the edge of the nest, the eggshell broke in its mouth and a chick tumbled out. The chick clambered back into the nest. The pine marten proceeded to remove other eggs and at the fourth visit, it took the hatched chick, before removing the last eggs. The pine marten must have dropped an egg at the edge of the nest (out of the view of the illuminated part of the nest), because when the female returned to the nest, an egg reappeared in the nest. It was not clear how the female retrieved this egg because it was dark, but she continued incubating and the egg hatched the following day.

Discussion

Our results from video and digital cameras indicated that 68% (42% for the adjusted value) of capercaillie nests at Abernethy Forest failed to hatch.

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Losses were mainly due to pine martens, which took 57% (33% for the adjusted value) of capercaillie clutches. These estimates provide an upper rate of loss if we do not adjust for the possibility that the video system attracted predators and a lower value if we correct for the possible influence of the video equipment. We suspect that the lower estimate of loss is more accurate because there was evidence from our experiment with artificial nests that the video equipment made nests more vulnerable to pine martens. We argue that the comparison between artificial and capercaillie nests is valid because it was highly likely that the pine marten was also the main predator of the artificial nests, since it was the sole predator filmed at 21 artificial nests during an earlier study in 1999 and 2000 (Summers et al. 2004). One possible explanation for the bias is that when pine martens encountered the cable between the camera and video recorder, they followed the cable to the nest. We were unable to test whether our daily visits to the video recorder (30-40 m from the nests) had any additional effect. The other possible predators of capercaillie clutches at Abernethy Forest are red fox and badger. Badgers are mainly localised on the northern border of the forest where it abuts farmland, so they were less likely to encounter capercaillie nests. They also leave all depredated eggs in and around a nest (N. Butcher pers. comm., N = 12), and this was not a feature of depredated nests (artificial or capercaillie) in our study. However, the absence of records of red foxes taking clutches could be that they shied away from the video installations. There is some evidence of foxes avoiding Trailmaster cameras in Texas, USA, because they were never photographed at nests, despite being present in the study area (Hernandez et al. 1997). However, using equipment similar to the present study, Bolton et al. (2007) filmed red foxes taking clutches of lapwings *Vanellus vanellus*. Trailmaster cameras are much bulkier than the video cameras we used, so there could be a difference in the response by red foxes to these camera systems.

Other studies of capercaillie nest loss, reviewed by Storch (2001), showed that loss can range from 6% to 86% (Table 1). The large inter-annual variation in loss of capercaillie nests in Norway was accounted for by changes in predator numbers and shifts in their diet according to the phase of the rodent cycle (Wegge & Storaas 1990). Specifically, capercaillie nest survival is higher when voles are abundant and predators are consuming mainly voles. The adjusted estimate of clutch loss in our study (42%) is within the mid-range for studies in mainland Europe and similar to earlier Scottish studies (38% and 39%) (see Table 1).

A notable deficiency in previous studies was the lack of information on the exact cause of nest loss. In Lindén's (1981) Finnish study, most losses (35%) were believed to be due to mammalian predators, 26% to avian predators, 14% to human disturbance and 9% to weather. In Germany, most losses (31%) were attributed to wild boar *Sus scrofa*, and the main avian predator was the jay *Garrulus glandarius* (Klaus 1985). In our study area, where red foxes are partially controlled and crows effectively controlled, we found that the pine marten was the main cause of nest loss. The pine marten was also identified as the main cause of chick mortality in Norway (Wegge & Kastdalen 2007).

The increase in pine marten numbers at Abernethy took place in the late 1990s, over a period when red foxes were being controlled. There is some evidence that pine marten numbers can be affected

Table 1. Nest loss of capercaillie in different studies. P = raw estimates of loss based on the percentage of failed nests found. M = loss based on the Mayfield (1975) method. The former method will be biased towards low estimates of nest loss. Note that the Norwegian studies probably shared some of the same data.

Place	Years	Percent lost	Sample size	Source
Finland	1946-52	6-16	1247	Siivonen 1953
Finland	1966-77	34^{M}	231	Lindén 1981
Scotland		38	24	Jones 1982
Thuringia, Germany	1971-75	35^{P}	32	Klaus 1985
Thuringia, Germany	1976-83	67^{P}		Klaus 1985
Varaldskogen and Vegårshei, Norway	1980-83	82^{P}	60	Spidsø et al. 1985
Varaldskogen, Norway	1979-86	$55\text{-}86^{M}$	174	Wegge & Storaas 1990
Pyrenees, France		45	15	Ménoni 1991
Bavarian Alps, Germany	1988-92	36^{P}	14	Storch 1994
Scotland	1950-98	39^{M}	43	Proctor & Summers 2002
Abernethy Forest, Scotland	2003-07	42^{M}	20	Our study

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by red fox predation (Lindström et al. 1995), so fox culling may result in more pine martens. However, Kurki et al. (1998) failed to find a negative effect of numbers of red foxes on those of pine martens. Furthermore, the culling at Abernethy largely affected fox cubs, and did not lead to a substantial decline in red fox numbers, as determined from scat counts (Summers et al. 2004). Therefore, we believe that the increase in pine martens was due to recolonisation of Abernethy after local extinction (Forsyth 1900, Gordon 1925), rather than to any reduction of red fox numbers.

Pine martens were once heavily persecuted by man in Britain, particularly during the 19th and early 20th centuries when many predatory birds and mammals were killed in an attempt to increase numbers of deer (Cervidae) and grouse (Tetraonidae) that could be shot for sport (Corbet & Harris 1991, Holloway 1996). Legislation to protect many predatory birds and mammals and the decline in the number of gamekeepers have resulted in predators, including pine martens, returning to former ranges and densities (Hudson 1992, Gibbons et al. 1993, Birks 2002). The expansion of woodland through extensive planting of conifer woods in the 20th century has probably also helped the spread of pine martens (Corbet & Harris 1991).

From the point of view of enhancing the natural biodiversity of semi-natural pinewoods in Scotland, the return of the pine marten must be welcomed. However, whether it is occurring at densities typical of present-natural woodland is debatable. The remaining fragments of semi-natural pinewood in Scotland have been managed for hundreds of years, either for timber, farming or sport shooting (Steven & Carlisle 1959, Fowler 2002). Therefore, the present structure of the woodland is not natural in terms of the relative composition of tree and shrub species. Analysis of pollen in cores of lake sediments has shown that there were more broadleaf trees and less heather 1,500 years ago (O'Sullivan 1973, 1977). Also, Abernethy Forest has old farm sites dominated by grasses. It has been noted in Fennoscandia that modern silviculture results in grasses colonising clear-felled areas, and this leads to high vole numbers that attract predators. This in turn leads to increased predation on ground-nesting birds (Hansson 1979, Angelstam 1992). Therefore, it is possible that the factors that determine the numbers and hunting patterns of pine martens are different in the semi-natural pinewoods of Scotland compared to natural pine forests. Although a study of the abundance of red foxes and pine martens in a fragmented boreal landscape found that there was strong evidence that fragmentation led to elevated predation pressure on ground-nesting birds by red foxes, the evidence against pine martens was weaker (Kurki et al. 1998). This is perhaps because pine martens favour older woodland and avoid the clear-cuts, which help create fragmentation (Storch et al. 1990). Nevertheless, a clearer understanding of how pine martens use semi-natural pinewoods in Scotland is required in order to implement management to reduce pine marten predation on capercaillie nests. Culling of pine martens is not an option because it is a protected animal (Birks 2002), but there may be ways in which the habitat can be manipulated to reduce pine marten numbers, thereby avoiding the constraints of predator control (Hewitt et al. 2001).

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