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Source: Wildlife Biology, 13(1): 19-27

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2007)13[19:MABCTU]2.0.CO;2

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Measuring avoidance by capercaillies *Tetrao urogallus* of woodland close to tracks

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Summers, R.W., McFarlane, J. & Pearce-Higgins, J.W. 2007: Measuring avoidance by capercaillies *Tetrao urogallus* of woodland close to tracks. - Wildl. Biol. 13: 19-27.

We carried out a study in four stands of Scots pines *Pinus sylvestris* at Glenmore Forest and Abernethy Forest, Scotland, to measure distances over which capercaillies *Tetrao urogallus* avoided woodland close to forest tracks (gravel roads designed for vehicles, but also used by recreational walkers and cyclists) during autumn and winter. Tracks with low and high human use were selected in the two forests, and the presence of capercaillie droppings under trees gave a measure of use for feeding at different distances from the tracks. At all sites, the use of trees by capercaillies was lower close to tracks. The amount of woodland effectively avoided by capercaillies ranged from 1 ha per 46 moftrack to 1 haper 82 moftrack at the different sites. Given the high density of tracks at Glenmore and Abernethy Forests (1,950 m/km² in both forests), the percentage of woodland avoided by capercaillies ranged within 21-41%. A likely explanation is that human activity in these small native pinewoods is disturbing capercaillies, and may reduce their carrying capacity. Possible microclimate or predator effects were discounted.

Key words: capercaillie, forest management, National Parks, pinewoods, Pinus sylvestris, recreational disturbance, Tetrao urogallus

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Received 26 July 2005, accepted 1 December 2005

Associate Editor: Ilse Storch

Although the proportion of people living in the British countryside is now less than in the past, the way in which people use the countryside has changed. Recreational use has increased markedly, and ease of access to once remote places means that human activities can occur virtually anywhere, including remote parts of Scotland (Warren 2002). However, some areas are subjected to particularly high public pressure due to their scenic and amenity values. The long existing in-

formal right of access to woodland for recreational walking in Scotland's countryside has recently been formalised through the Land Reform (Scotland) Act 2003, and the Scotlish Outdoor Access Code. This can place a requirement on managers of these areas both to make recreational opportunities available and ensure that sites (soil and vegetation) are not damaged and that wildlife is not put at risk. In particular, management of areas for conservation needs to take into

account the fact that many animals do not tolerate the close presence of people and seek undisturbed areas (Fernández-Juricic et al. 2001, Woodfield & Langston 2004). If disturbance reduces the carrying capacity, then conservation areas need to be larger to support a self-sustaining population or meta-population than they would be without disturbance.

Many natural and semi-natural habitats, particularly woodland, are crossed by tracks, gravel and asphalt roads. The roads were originally built for vehicles, but are often used by walkers and cyclists. While some species may benefit from the open corridors in woodland created by tracks, the tracks can create barriers for others (Forman & Alexander 1998), effectively fragmenting the forest. Tracks and roads also allow access to people, sometimes to more people than originally intended. Thus, the upsurge in recreation has meant that people now regularly visit areas rich in wildlife, using tracks originally intended for other purposes. In some cases, this has resulted in wildlife avoiding the vicinity of tracks and roads. Most studies where birds have been shown to avoid people, refer to birds of open country or wetlands (Woodfield & Langston 2004). For example, golden plovers Pluvialis apricaria avoided areas up to 200 m from the Pennine Way (a popular walking route in north England) during the chick-rearing period (Finney et al. 2005). Less is known about the effects of human presence on woodland birds. Large birds and mammals are of particular concern because of their special status, either as top predators, key-stone species, indicator species or umbrella species (Thompson & Angelstam 1999, Suter et al. 2002).

The capercaillie *Tetrao urogallus* is one such species for which human disturbance associated with recreation has been partly implicated in the declines in western Europe (Mueller 1981, Leclercq 1985, Menoni 1994, Brenot et al. 1996, Palanque 1999). In Scotland, the status of the capercaillie is of conservation concern due to the large decline in population size since the 1970s and small extent of the main habitat, old Scots pine Pinus sylvestris forest (Anon 1995, Wilkinson et al. 2002). This led to a number of conservation initiatives, including the removal or marking of forest fences against which birds were dying when flying into them (Baines & Summers 1997), and the creation of new native woodland (Mason et al. 2004). However, the extent to which human use of forests affects capercaillies is unknown. This is of particular concern within the recently formed Loch Lomond and Trossachs National Park and Cairngorms National Park, both of which contain concentrations of capercaillies. The latter also contains the largest remaining fragments of native pinewood, which are of particular value for this species, having higher densities of capercaillies than conifer plantations (Catt et al. 1998, Wilkinson et al. 2002). Such native pinewoods are also of greater scenic value than plantations and tend to be more heavily used by walkers and cyclists.

A recent study of the winter dispersion of capercaillies at Abernethy Forest reserve, Scotland, showed that, in addition to certain vegetation characteristics, capercaillies preferred to feed in trees more distant from forest tracks than one would expect if their dispersion were random (Summers et al. 2004). These tracks were used the year round mainly by visitors who walked or cycled, and by reserve staff in vehicles. The avoidance of woodland close to tracks by capercaillies was interpreted as being due to the effects of human disturbance, and occurred in spite of attractive attributes of tracks, such as sites for gritting and dust bathing, and puddles for drinking (Summers et al. 2004). In a natural forest, capercaillies obtain grit at root plates and by streams. However, their study was not primarily designed to examine track avoidance and gave no information on how any effect of disturbance varies with distance into the forest, nor whether the effect differs between tracks that have high and low intensities of human use. Our study was designed to test this hypothesis more rigorously by comparing woodland close to tracks with different levels of human use, and thereby help forest managers decide on land management consistent with the conservation of the capercaillie in Scotland. In addition, we considered whether the avoidance of woodland close to tracks was due to factors other than human disturbance. For example, microclimate varies with distance from forest edges (Matlack & Litvaitis 1999), and the gap created by a track may be regarded as an edge. Alternatively, woodland tracks may be avoided if predators hunt along tracks. Therefore, we also set out to test whether microclimate or predators were causing capercaillies to avoid woodland close to tracks. One possibility that was not investigated was that capercaillies avoid woodland close to tracks because they avoid open spaces.

Methods

Our study was carried out in Glenmore Forest (57°10'N, 3°40'W) and Abernethy Forest (57°15'N, 3°40'W) in the Cairngorms National Park, Scotland (Fig. 1), during winter 2003/04 (26 November 2003-

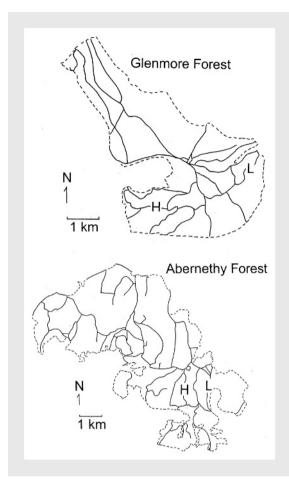


Figure 1. Outlines (----) of Glenmore Forest and Abernethy Forest showing tracks and roads (—). The selected study sections of tracks with low (L) and high (H) visitor use are shown.

10 March 2004). We chose four tracks (two sites within each of the two forests) through native Scots pine woodland containing capercaillies. Track choice was based on knowledge that capercaillies used the adjoining woodland, that the stand type was similar within a site and that two contrasting levels of human use (low and high use) could be found in each of the two forests. At Abernethy Forest, information on visitor use was based on questionnaires from visitors (Summers 2000). During single weekend days in February, March, May and August 1999, the numbers of groups of people that walked or cycled along the heavily used track were 2, 7, 31 and 13, respectively. The corresponding figures for the lightly used track were 0, 0, 3 and 0, respectively. Thus, the pattern of use across the forest did not vary seasonally, only the magnitude of use. The average group size of walkers was two, of whom 21 and 26% were walking with pet

dogs in two parts of the forest. The percentage of groups cycling varied between 4 and 18% for different dates. The average amount of time spent in the forest by any group was about 1-2 hours, and visitors rarely strayed from tracks, perhaps because of the tall heather Calluna vulgaris and uneven ground within the wood, and the presence of ticks *Ixodes* sp. on the vegetation, at least between spring and autumn. Vehicle use by reserve staff was not recorded (Summers 2000). The most heavily used track at Abernethy could not be used as a study site because surveys showed that there were too few capercaillies in the adjacent woodland. At Glenmore Forest, the level of use of tracks was inferred from the category of track (e.g. dead-end tracks with no formal recreation attraction were regarded as lightly used, and way-marked tracks for walking and cycling represented high use). In order to confirm these categories, people at Abernethy and Glenmore Forests were counted when data were being collected on trees closest to the tracks. All counts were made during weekdays and therefore not influenced by weekends when numbers would have been higher.

Sites were chosen with a similar stand structure within a site. To support the classifications, tree size (diameter at breast height; DBH) was measured for the trees searched for capercaillie droppings. This also allowed tree size to be included as a potential explanatory variable, because capercaillies prefer larger trees (Summers et al. 2004).

At 25-m intervals along each track, 16-20 250-m long transects, running into the woodland perpendicular to one side of the track, were walked. At 10-m intervals along each transect, the nearest pine tree > 5 m in height was selected and the area under the crown searched for capercaillie droppings for a maximum of three minutes to determine whether capercaillies had fed there. Droppings from feeding capercaillies tend to be scattered under the crown whilst droppings from roosting birds are concentrated. The latter, however, were much rarer and ignored. Capercaillie droppings in pinewoods in winter are composed of the remains of pine needles (Summers et al. 2004), and may survive several months. Therefore, presence of droppings under a crown indicated that capercaillies had fed there within the past few months.

To examine possible microclimate effects at different distances from the track, temperature and wind speed were recorded at 25-m intervals along 10 transects perpendicular to the track and to a distance of 250 m into the woodland at the two Abernethy sites. The transects were 25 m apart and surveyed at each site on windy days between 23 December 2004 and 11

January 2005. A Kestrel 3000 anemometer (Richard Paul Russel Ltd.) was mounted on a 4.5-m pole and the following measurements made at each recording point: air temperature, average air speed and maximum gust over a three-minute period. The data were analysed using 2-way ANOVAs, with the transect effect introduced before the distance bands into the woodland.

Aerial predators of capercaillies, such as golden eagle *Aquila chrysaetos* and goshawk *Accipiter gentilis*, could potentially cause capercaillies to avoid woodland close to tracks if they hunted along woodland corridors created by tracks. Therefore, the presence of these raptors was to have been noted; but, in fact, none was seen. Ground predators were not considered because capercaillies feed mainly in the canopy throughout the autumn and winter in Abernethy Forest (Summers et al. 2004).

Analyses of the data on the percentage of trees with droppings under them were conducted in SAS version 8 (SAS Institute Inc. 2001) in two stages. Initially, the PROC GLM was used to produce a generalised linear model (GLM) combining data from all four sites. The dependent variable was the percentage of trees used across all sampling points at a given distance from the track (which exhibited a normal distribution), with forest (Abernethy; Glenmore), human use (low, high; both two-level factors), DBH and distance to the track (both covariates) included as explanatory variables. To model the potential for a non-linear relationship between dropping occurrence and distance to the track, the quadratic term for distance was also incorporated in the analysis. Model selection was by backwards deletion of non-significant (P > 0.05) terms from a full model, in which first-order interaction terms were also considered.

A biologically plausible shape for the relationship between percentage use of trees by capercaillies and distance to track (*cf.* Summers et al. 2004) would be one in which tree use increases to an asymptote and then levels off as a plateau. To model this explicitly, we additionally fitted segmented models to the data, using the NLIN procedure in SAS version 8 (SAS Institute 2001). This models a standard quadratic relationship between x and y, when $x < x_0$, and constant values of y where $x > x_0$; x_0 is the value for x at which y reaches a plateau, and is estimated within the NLIN procedure (SAS Institute Inc. 1990:1162). Because it is not possible to assess the significance of individual terms using the NLIN procedure, we simply modelled the terms that remained in the original GLM. To aid subsequent interpretation, track densities at Glenmore and Abernethy Forests were calculated from 1:50,000 Ordnance Survey maps, excluding foot paths.

Results

Tree sizes

At both Abernethy sites, there were significant differences in mean DBHs among the distance bands ($F_{24,384}=4.17$, P<0.001 for high use, and $F_{24,223}=2.36$, P=0.001 for low use). At the site with high human use, trees were smaller at greater distances from the track (r=-0.79, P<0.001), whereas the trees at the site with low human use were larger at greater distances from the track (r=0.36, P<0.001). At Glenmore Forest, there were no significant differences in the mean DBHs among distance bands ($F_{24,373}=0.94$, P=0.548 for high use and $F_{24,347}=1.39$, P=0.109 for low use).

Counts of people and predators

The numbers of people counted during the study are shown in Table 1. Five of the visitors at Abernethy (high use) were cyclists, and there were eight dogs. Although the counts are small, the figures confirmed our initial classification into sites with high and low human use, and they showed broadly similar amounts of human activity in the two forests for the given categories of use.

No golden eagles or goshawks were seen.

Table 1. Numbers of visitors and dogs (in brackets), model characteristics and estimates of woodland effectively avoided by capercaillies, based on the model presented in Table 3.

Forest and category of human use	Number of visitors (dogs)	Distance to asymptote (m)	Proportion of area above the curve	Effective distance avoided by capercaillies (m)	Length of track (m) related to 1 ha of wood effectively avoided	Effective area (ha) of woodland avoided per 100 ha
Abernethy - high	20 (4)	197	0.37	73	68	26
Abernethy - low	6(0)	197	0.31	61	82	21
Glenmore - high	11(3)	291	0.37	108	46	41
Glenmore - low	5(1)	291	0.22	64	78	23

Table 2. Results of 2-way ANOVAs on microclimate data for sites with high and low human use at Abernethy Forest. Sample sizes were 110 for both sites.

		Transect effect		Distance band from track	
Human use category	Mean value (SD)	df F(P)		df F(P)	
High					
Temperature (°C)	7.0 (0.94)	9	148.4 (< 0.001)	10	0.35 (0.97)
Average wind speed (m sec ⁻¹)	1.07 (0.54)	9	13.7 (< 0.001)	10	0.24(0.99)
Maximum wind speed (m sec ⁻¹)	1.60 (0.69)	9	5.65 (<0.001)	10	0.56 (0.845)
Low					
Temperature (°C)	8.2 (0.47)	9	48.3 (<0.001)	10	0.39 (0.95)
Average wind speed (m sec ⁻¹)	1.5 (0.70)	9	35.08 (<0.001)	10	0.74(0.69)
Maximum wind speed (m sec ⁻¹)	2.4(1.02)	9	19.62 (< 0.001)	10	0.63 (0.79)

Microclimate

Data on temperature and wind speed were obtained at the two sites in Abernethy on four windy days, when the mean wind direction was 219° and 185° for the sites with high and low human use, respectively. In all six data sets, there were significant transect effects indicating changes in weather during the survey period, but there was no effect of distance from the tracks for any of the microclimate variables (Table 2).

Modelling capercaillie use of trees at different distances from tracks

Use of trees by capercaillies differed significantly between forests ($F_{1,92} = 6.84$, P = 0.0104), and with levels of human use ($F_{1,92} = 27.75$, P < 0.0001), being less at higher levels of human use (Fig. 2). As expected, there was a significant positive correlation between tree use by capercaillies and DBH ($F_{1,92} = 10.15$, P = 0.002). A curvilinear relationship with distance to track ($F_{2,92} = 10.15$), where $F_{2,92} = 10.15$, $F_{2,92} =$

33.91, P = 0.0002), including both linear and quadratic terms demonstrated an increase in tree use away from tracks. The shape of this relationship differed significantly between the two forests with regards to both the linear ($F_{1,92} = 6.34$, P = 0.0136) and quadratic ($F_{1,92} = 4.44$, P = 0.0378) terms. There was no significant effect of category of human use upon the shape of this relationship.

To produce more biologically plausible models, we manipulated this existing model of tree use to fit an asymptotic relationship between tree use and distance to track (see Methods). The significant effects of DBH, forest and human use remained in this model, indicating that the intercept for tree use was lower at Abernethy Forest than at Glenmore Forest, and there was greater tree use by capercaillies at the sites with low human use than at sites with high human use (see Fig. 2, Table 3). The slope of the relationship between tree use and distance differed significantly between

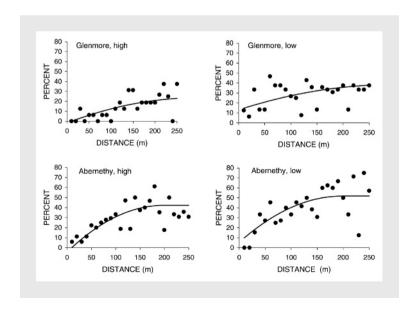


Figure 2. Percentage of trees with capercaillie droppings at different distances from the tracks (gravel roads) at Glenmore Forest and Abernethy Forest where use by visitors was classed as high and low. Curves were fitted according to the model presented in Table 3.

Table 3. Parameter estimates for a model of the percentage of trees with droppings under the crowns of Scots pines in relation to distance from track and diameter at breast height (DBH) for two forests and two categories of human use. To allow the relationship between tree use and distance from track to asymptote, a segmented model was used (see text). From the segmented model, the distance from the track at which the asymptote in tree use was reached was 197 m for Abernethy Forest and 291 for Glenmore Forest. Glenmore Forest = 0, Abernethy Forest = 1, Low human use = 0, High human use = 1.

Parameter	Estimate	SE 95% confide		dence limits
Intercept	-3.47	7.16	-17.70	10.75
Distance	0.17	0.086	-0.00014	0.34^{a}
Distance ²	-0.00029	0.00032	-0.00093	0.00034^{a}
DBH	0.50	0.16	0.18	0.811
Forest	-21.14	8.14	-37.30	-4.99
Human use	-11.50	2.18	-15.83	-7.16
Distance*forest	0.30	0.11	0.078	0.52
Distance ² *forest	-0.00089	0.00038	-0.0016	-0.00015

^a Although the confidence intervals for the linear and quadratic terms for distance overlap zero, this is a consequence of the inclusion of the interactions of these terms with forest, which were significant.

forests, increasing more steeply at Abernethy than at Glenmore Forest, indicative of greater mean tree use at Abernethy over the entire transect length. The distance at which use of trees reached an asymptote differed between forests; 197 m at Abernethy and 291 m at Glenmore Forest (see Fig. 2). Note that the asymptotic distance for Glenmore was estimated to be slightly beyond the limit of sampling.

It is difficult to assess the results from the different curves in terms of the amount of woodland avoided by capercaillies (see Fig. 2). Therefore, in order to make directly comparable measurements, the proportion of the area above the curved line up to the asymptote was calculated for each site. These were then multiplied by the distances to the asymptotes from the model (see Table 3), and avoidance can be reinterpreted as a step model in which capercaillies totally avoid woodland up to a certain point after which there is no avoidance (Fig. 3). The distances into the forests from the tracks over which capercaillies were effectively avoiding totally ranged within 61-108 m. Considering both sides of the track, this implies that 1 ha of woodland was avoided by capercaillies for every 46-82 m of track (see Table 1). These distances were then converted into areas of woodland avoided, based on the track plus road densities at the two forests; 1,950 m/ km² at both forests. Therefore, the area of forest effectively avoided by capercaillies at Abernethy Forest was 21/100 ha under conditions of low human use and 26/100 ha under high human use. The corresponding values for Glenmore Forest were 23/100 ha under low human use and 41/100 ha under high human use (see

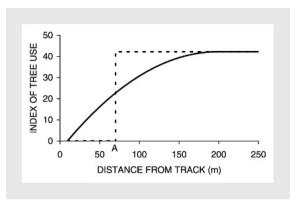


Figure 3. Index showing tree use by capercaillies within woodland at Abernethy Forest where the adjacent track had high human use. The solid curved line expresses the gradual increase in tree use by capercaillies out to 197 m where an asymptote was reached (i.e. where there was no further indication of avoidance; see Fig. 2). The dashed line is a simplification of the same data and shows the distance (point A at 73 m) at which the index of tree use could be considered to switch from zero to its maximum value. This value provides an estimate of avoidance that can be directly compared between sites.

Table 1). These calculations took into account the tracks or roads that had woodland on only one side, and where bands of avoidance overlapped at track or road junctions and intersections.

Discussion

Our results confirmed the earlier work of Summers et al. (2004) that capercaillies avoid trees close to tracks (gravel roads). They also showed that tree use was lower close to tracks with higher levels of human use. These results are consistent with the idea that human disturbance causes the birds to avoid woodland close to tracks. It also supports anecdotal observations that capercaillies are rarely seen by visitors to the forest, except early in the morning when birds are flushed from tracks which are used by capercaillies for gritting and dust-bathing.

Other possible causes for avoiding trees near tracks were that the microclimate was poorer close to tracks or that capercaillies could be vulnerable to aerial predators that use the tracks as hunting zones. However, we found no changes in microclimate at different distances from the track. This may be due to the open nature of the woodland, such that the open corridor due to the track was not an unusual gap feature, apart from it being linear. Likewise, there was no indication that predators caused capercaillies to avoid woodland close to tracks. The only potential aerial predators of

capercaillies, the golden eagle and goshawk, are rarely seen in the forest (a few records per year, and none was seen during our study). Although golden eagles breed in Abernethy Forest, they generally hunt over adjacent moorland. The goshawk is rare at Abernethy, and is not known to have nested there in the last 10 years, though it is occasionally seen. Also, the open nature of native pinewoods would allow goshawks to hunt through the woodland, rather than being restricted to corridors and rides as may be the case in dense plantations.

It is important to quantify whether avoidance of woodland close to tracks affects bird density (Gillet al. 1996). During the period between September and July, capercaillies at Abernethy Forest derive most of their diet from Scots pines (pine needles from September to April and male cones during May to July; Summers et al. 2004). Thus, if avoidance reduces the availability of trees near to tracks, some of the potential food resource in the wood is unavailable. Studies in Norway and Scotland indicate that loss of old conifer woodland can have a negative effect on capercaillie numbers. The number of male capercaillies associated with a lek declines as the percentage of old forest within 1 km of the lek decreases (Wegge & Rolstad 1986, Picozzi et al. 1992). Leks tend to be about 2 km apart, so a 1-km radius around a lek will encompass most of the males' territories around the lek. There is an associated increase in territory size as the percentage of old forest declines (Wegge & Rolstad 1986). Therefore, by reducing the amount of old woodland available to capercaillies, tracks could reduce the overall population size.

Capercaillie densities in Scottish native pinewoods of 2.7-5.0 birds/km² in the winters of 1992/93 and 1993/94 (Catt et al. 1998) and 1.63/km² in the winter of 1998/99 (Wilkinson et al. 2002) are typical for many woods in the range of the capercaillie (1-3/km²; reviewed by Storch 2001), but are lower than autumn densities of 5 and 10 per km² found in the better Scandinavian woods (Sjöberg 1996). Although these density estimates from Scotland and Scandinavia were derived at different seasons, the difference cannot be wholly accounted for through mortality between autumn and winter (Moss et al. 2000). The difference implies that the potential to increase capercaillie densities in native pinewoods in Scotland exists. However, more research is required specifically to examine the link between capercaillie numbers and the availability of food.

Glenmore Forest and Abernethy Forest comprise a mixture of native pinewoods and conifer plantations

owned and managed by the Forestry Commission (Scotland) and the Royal Society for the Protections of Birds, respectively. Both forests are renowned for their high scenic qualities, by comprising semi-natural woodland in a mountainous setting. There is an open visitor policy and both attract thousands of visitors who make an important contribution to the local economy each year (Macmillan 1995). At Glenmore Forest, visitors are encouraged through the provision of recreational facilities for camping, water-sports, skiing, cycling and mountaineering. Approximately 350,000 visit the area annually (D. Jardine, pers. comm.). Abernethy Forest is less overtly promoted for recreation but, nevertheless, attracts thousands of tourists, walkers and bird-watchers each year. Over 35,000 people visited the interpretation and viewing centre by Loch Garten in Abernethy Forest between April and September 2003 (Taylor & Williams 2004), though the number visiting the whole forest will have been larger. Although human use was not measured in detail during our study, it would be useful to describe how numbers of visitors vary across both forests, and through the year, because the level of disturbance to breeding birds can be a function of both distance and the number of people involved (Beale & Monaghan 2004). Thus, there may be additional effects of disturbance in the summer when capercaillies and their chicks feed mainly on dwarf shrubs and insects (Sjöberg 1996), and visitor numbers are higher (Summers 2000).

Assuming that the tracks in this study are representative of other tracks within the forests, it is clear that large areas of woodland (21-41%) may be avoided by capercaillies as a result of disturbance. This largely results from the high track densities at Glenmore and Abernethy Forests (1,950 m/km²). These track densities are at the upper part of the range within conifer plantations, where densities are typically 1,000-2,000 m/km² in Britain (Blatchford 1978). Although track densities at Abernethy Forest have been high since the late 19th Century (O'Sullivan 1973), it is likely that only recently have they been utilised by large numbers of visitors, because most of the forest was formerly a private estate without a policy of visitor promotion, before becoming an RSPB nature reserve in 1988.

Native pinewoods support higher densities of capercaillies than do plantations (Catt et al. 1998, Wilkinson et al. 2002). They are also attractive to people because of their scenic qualities and receive larger numbers of visitors than most plantations where track densities are lower and access to visi-

tors is not promoted. As a result, disturbance may be particularly acute for capercaillies in native pinewoods, because the localities that support the greatest numbers of capercaillies also attract the most people. Both Glenmore and Abernethy Forests are renowned for their wildlife, capercaillies included. and parts have been designated as Sites of Special Scientific Interest, Special Protection Areas for capercaillies and Natural Nature Reserves (Abernethy Forest only). They also fall within the Cairngorms National Park. Therefore, consideration should be given to the current density and placement of tracks. Unnecessary tracks could be removed, rerouted or their promotion or maintenance reduced. Such steps should be made by managers in consultation with people who use the forests to ensure that any changes strike the right balance between the conservation and amenity objectives. Management to reduce disturbance can produce rapid recoveries in bird habitat use (e.g. Finney et al. 2005), and our study suggests that this could increase the availability of woodland to capercaillies. An example of such management, through the destruction of 70 km of forest tracks in the Bayerischer Wald National Park, Bavaria, to create a 'wildlife protected area', resulted in capercaillies returning to the surrounding woodland after two years (Scherzinger 2003).

Acknowledgements - our project was funded by Forestry Commission Scotland and Scottish Natural Heritage. The Forest District Manager (D.C. Jardine) at Glenmore Forest and Senior Site Manager (C. McClean) at Abernethy Forest provided access permission. R. Proctor made the microclimate readings. A. Amphlett, Dr D.W. Gibbons, M. Hancock, D.C. Jardine, K. Kortland, C. McClean, Dr C. Quine, S. North and Dr J. Wilson commented on the draft of this paper.

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