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Leisure activities in fragmented western European forests are thought to threaten local populations of capercaillie *Tetrao urogallus*. We studied impacts of human disturbance on capercaillie in three Scottish woods by documenting the distribution of their droppings in relation to woodland tracks and entrances, surrogates for human activity. Droppings were sparser within 300–800 m of entrances and 70–235 m of tracks, depending on track use and habitat. Some 75% of each wood lay within 130 m of a track. In the most disturbed wood, droppings were most abundant in the centres of larger patches of trackless boggy ground, which acted as refuges. The reproductive rate (chicks reared per hen) at our three study areas was no less than in other, less disturbed parts of the same valley. The ratio of full-grown hens to cocks, however, was unusually low in the two most disturbed woods. Disturbance reduces the birds' living space, possibly affecting hens more than cocks. It might therefore impact metapopulation dynamics and contribute to genetic impoverishment in small populations. Ensuring that people and dogs keep to tracks, closing tracks and creating refuges should mitigate such effects.

Tourism and outdoor recreation threaten biodiversity and the very survival of some endangered species (Czech et al. 2000, Sutherland 2007, Juutinen et al. 2011, Steven et al. 2011). Capercaillie *Tetrao urogallus*, largest game bird of Western Palaearctic boreal and montane forests, maintains much of its original range, but serious declines in western, central and southeastern Europe have resulted in local extinctions. Here, most remaining populations live in remnant patches of coniferous forest surrounded by agriculture or built development (Storch 2007). Such woodland often attracts tourists and sportsmen, such that leisure activities can seriously threaten local populations (Thiel et al. 2011).

In Scotland, after a big decline in the last quarter of the 20th century (Catt et al. 1998), the population has remained at 1000–2000 birds during the 21st century (Eaton et al. 2007, Ewing et al. 2012). Over most of its range, however, the bird has become increasingly sparse, such that about 75% of the population is now in the Spey valley (Ewing et al. 2012). At the same time, this valley has become increasingly popular for tourism, recreation and housing since the establishment of the Cairngorms National Park in 2003 (CNPA 2011). To manage this conflict, we need to understand what does and does not disturb capercaillie, and what aspects of disturbance impact the birds' population dynamics.

Summers et al. (2007) showed that capercaillie in the Spey valley avoided woodland near vehicle tracks, presumably due to associated disturbance. Disturbed birds that move elsewhere may thrive just as well. On the other hand, movement to less disturbed habitat may result in increased density there, so impacting vital rates (Gill et al. 2001).

In southern Germany, disturbed capercaillie had elevated levels of the stress hormone corticosterone (Thiel et al. 2008), which might affect their fitness. In addition, movement associated with natal dispersal in Scotland resulted in heavier mortality from capercaillie flying into forest fences (Moss et al. 2000) – the same may happen when birds move due to disturbance.

Impacts of disturbance on grouse populations might be reduced by refuges (Braunisch and Patthey 2011). However, the effectiveness and design of grouse refuges remains a matter of informed conjecture (Suchant and Braunisch 2004).

Here we examine how capercaillie droppings are distributed in relation to surrogates for human disturbance: woodland entrances and tracks. We compare the demography of capercaillie in much disturbed versus less disturbed woods, and discuss the potential role of undisturbed refuges as mitigation.

Material and methods

Study areas

Capercaillie are rarely seen in some much disturbed woods in the Spey valley. Our three main study areas (Fig. 1, 2) still held birds despite manifest disturbance from a network of tracks. These included vehicle tracks, which were gravelled, built primarily for forestry vehicles, but also used by walkers > cyclists > horse riders; and footpaths, which were used little or not at all by vehicles, mostly narrower than vehicle tracks, some improved with gravel, others unimproved desire paths (Fig. 2). Some 75% of the ground in each study area was within 130 m of a track (Fig. 3).

Boat of Garten Wood (studied area 273 ha, 57°14′N, 3°46′W, Fig. 2) lies next to Boat of Garten, a Highland village and tourist centre with about 500 residents. The privately-owned woodland is mostly planted and self-sown Scots pine *Pinus sylvestris* with juniper *Juniperus communis*, the understory dominated by heather *Calluna vulgaris*, bilberry *Vaccinium myrtillus* and cowberry *Vaccinium vitis-idaea*. It is used by villagers and tourists for dog-walking, rambling, running, cycling, horse-riding and foraging for mushrooms and berries. The study area was bounded by a road to the north, a railway to the southeast and less-used woodland to the west.

Anagach Woods (356 ha, 56°59′N, 3°30′W, Fig. 2) is a community woodland by Grantown-on-Spey, a Highland town and tourist centre with about 2100 residents. The wood is used for recreation, as at Boat of Garten. Originally planted in the 18th century, it now resembles native pine woodland, as at Boat of Garten. It includes nine areas of bog woodland (1.3–28 ha) with open water for much of the year. Tracks are mostly on dry ground. Study boundaries largely coincided with those of the community woodland.

Glenmore Forest (study area 411 ha, 57°10′N, 3°40′W, Fig. 2), a multi-purpose forest planted mostly with Scots pine, is managed by the Forestry Commission and has an all-year caravan and camping site with over 200 stances just to its northeast. It lies within Glenmore Forest Park, itself a year-round tourist attraction and visitor centre that encourages ramblers, joggers, dog-walkers, cyclists, horse-riders and cross-country skiers. Less frequent, off-track, activities include snowshoeing, orienteering, foraging and deer control. The study area was bounded by Loch Morlich and tributary stream to the north, fences to the south and west, and a public road plus a stream to the east.
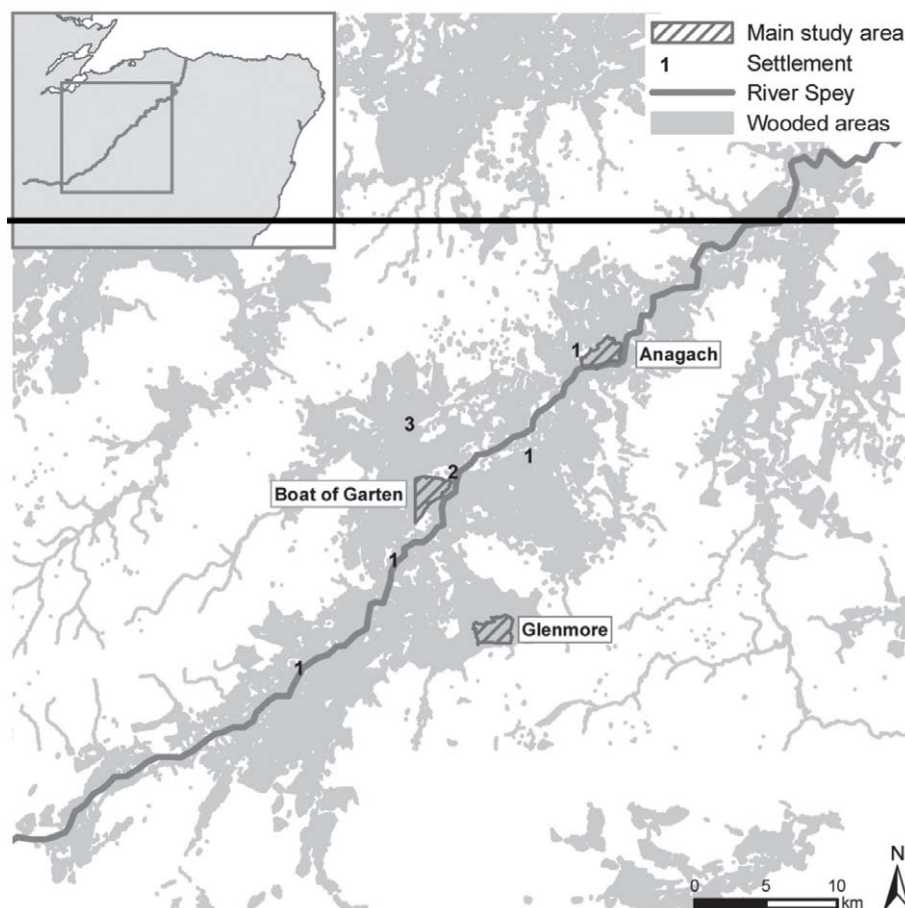
Figure 1. Study areas in the Spey valley. Main areas are labelled; subsidiary ones are near numbered settlements, the numeral indicating the number of subsidiary areas. From north to south, settlements are Grantown, Carrbridge, Nethybridge, Boat of Garten, Aviemore, Kincraig. Inset: mapped area in relation to River Spey and coastline of northeast Scotland. The mapped part of the valley contains about 75% of the capercaillie in Scotland. Contains Ordnance Survey data © Crown copyright and database right 2012.

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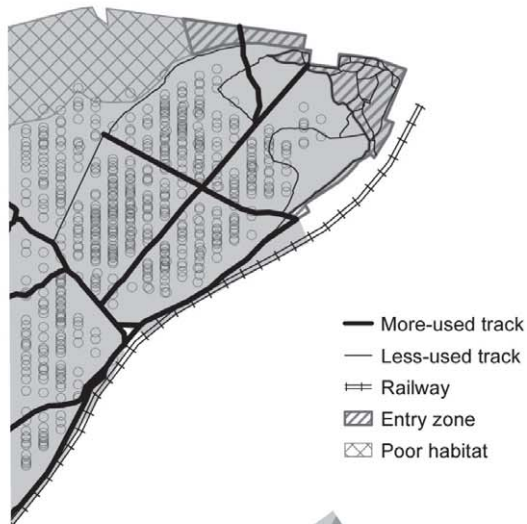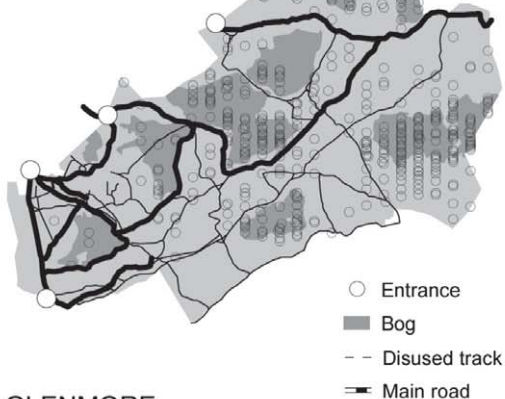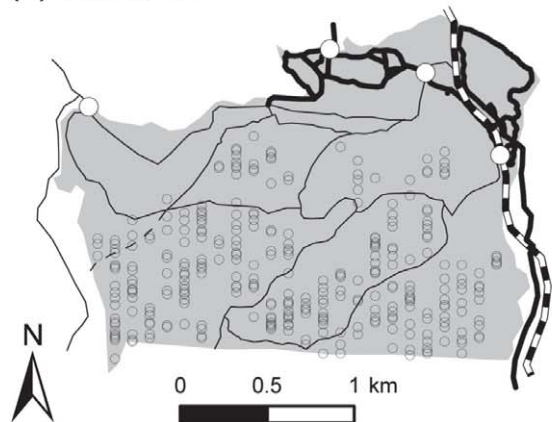
Figure 2. Main study areas. Ground searched in light grey. Droppings (O), some observations superposed. The patch of poor habitat at Boat of Garten, a grassy field, was covered by transects but otherwise excluded from the study.

People and dogs on or off leashes follow tracks but may range off them, especially when adjacent ground is flattish, so creating narrow desire paths. Terrain at Boat of Garten is flattish. At Anagach, glacial landforms create some small scale topography, but the main obstacle to walking off tracks

is bog woodland. Glenmore has more natural relief plus widespread silviculture, uneven terrain due to old drainage ditches and ploughings, brash, and patches of thick regeneration. In addition, many walkers, heading through the wood to higher ground in the south, are less likely to leave tracks than those who linger on the flatter and more accessible terrain in the north.

Counts of cocks, hens and well-grown chicks in late summer (brood counts) were done at 12 woodland sites in the Spey valley (Fig. 1). These included the three main study areas (Fig. 2), where ground counted over was within (Anagach), much the same as (Boat of Garten), or partly the same as and partly contiguous with (Glenmore) the area used to survey droppings. Another nine subsidiary areas served as less-disturbed comparisons.

Surveying droppings

We surveyed droppings between April 2006 and September 2010, on five (eight at Boat of Garten) occasions ('surveys') at each area, at all seasons. Hand-held GPS units with manufacturers' specified accuracies of 6–15 m were used to navigate and record positions. Bird sign was noted along 4 m wide N–S transects crossing each study area at 100 m intervals (Table 1). On encountering a group of droppings, the observer recorded their position, number and apparent sexual provenance (Appendix 1). When there was no clear gap between one group and the next (< 10% of records), a new record was started 25 m from the previous encounter. Birds (cock, hen, adult of unknown sex) were noted.

Entrances, tracks, distances and habitat

People, dogs, horses and vehicles entered each wood from one main direction. At both Anagach and Glenmore there were four main gated entrances, and the distance (m) of a location from the nearest entrance was 'distance from entrance' (dE, Table 2). Boat of Garten had many points of entry from the village at its north-eastern edge, near which no droppings were recorded (Fig. 2), so here we defined an 'entry zone' from which to measure dE. At Glenmore, elevation rose with dE but the two were highly correlated (Pearson $r_{2084} = 0.90$) and so there was no need to model elevation separately.

Positions of the main tracks were taken from Forestry Commission maps and Google Earth. Others were recorded using hand-held GPS units. The distance between a location and its nearest track was 'distance from track' (dT).

The network of tracks at each study area was classified into two 'classes': more-used and less-used (Table 3). A third class, at Glenmore only, comprised a blind 500 m 'disused' section of track (Fig. 2), previously much used by vehicles and people but currently by only an occasional walker or cyclist. We used this natural experiment to predict that the disused section would not depress the 'probability of finding droppings' (Pf).

Variations in Pf did not usefully correspond with forest compartment maps, evidently because relevant variations in habitat were more fine-grained than compartments. On the bogs at Anagach (Fig. 2), however, droppings were much more abundant than on dry ground. Hence we included
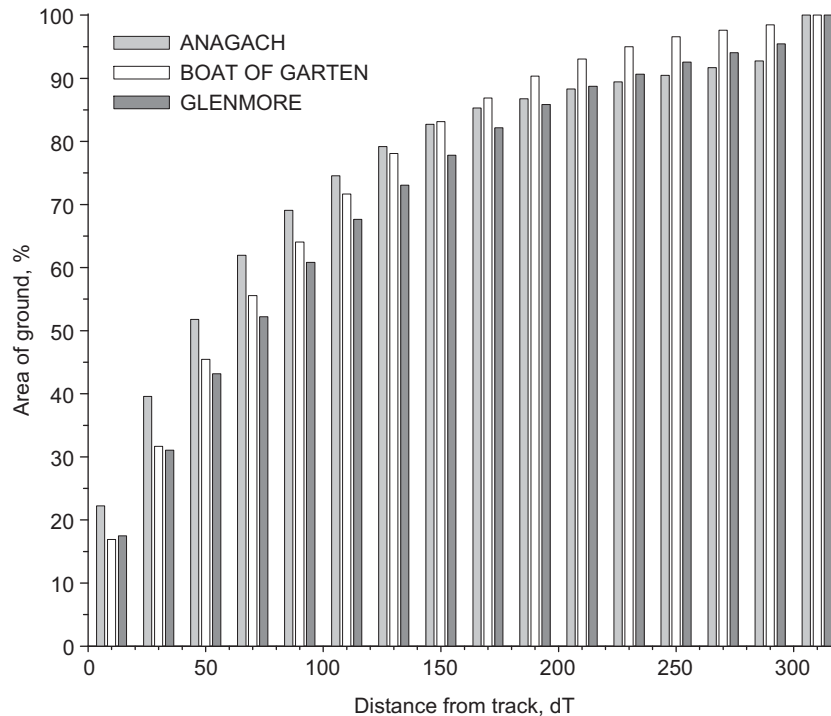
Figure 3. Percentage of each study area within various distances from a track. Cumulative distribution in 20 m bands, right hand bars ≥ 300 m.

dry/boggy ground as a category in models. Of nine separate bogs, three comprised two boggy patches joined by a narrow neck, so we defined 12 boggy patches of 1.3–12 ha. The centre of each patch, estimated by eye on the map, was located as far as possible from all points at its edge. For each grid location in a patch we measured 'distance from nearest bog edge' (Be) and 'distance from bog centre' (Bc).

Demography and disturbance

Brood counts, in late July and early August 2006–2011, involved searching 12 sites (Fig. 1) for capercaillie hens and chicks, with trained dogs (Moss and Oswald 1985). Adult cocks, encountered incidentally, were also recorded. From counts, we calculated reproductive rate (chicks per hen) and sex ratio (adult cocks per hen) at each site. These counts were part of an ongoing monitoring of the Scottish capercaillie population (Baines et al. 2011).

Currently, the idea of 'disturbance' to capercaillie is intuitively obvious, easy to define (interruption of a settled and peaceful condition) but difficult to measure. We therefore

used the expert judgement of two professional capercaillie managers, past (KK) and present (TP) Capercaillie Project Officers (FCS 2008) respectively. Each had years of experience at all 12 sites, which they ranked for disturbance. RM tasked them to do this without communicating with each other, giving no prior warning or definition of disturbance. Responses were immediate with no methodological questions. The sole caveat (KK) was that, except for Anagach and Boat of Garten, even the most disturbed areas included tracts of 35–300 ha that had few tracks or visitors, and were used by capercaillie.

Statistical modelling

Spatial distribution of droppings
Field observations comprised locations of droppings. Models compared locations with and without droppings. Locations were therefore redefined as all the intersections of a grid with N–S lines overlying the transects, and E–W ones at 20 m intervals. Each record of droppings was allotted to its nearest grid location, leaving unfilled locations for comparison.

Table 1. Summary of observations (number of transect-based surveys).

	Boat of Garten (8)		Anagach (5)		Glenmore (5)	
	Droppings[a]	Birds[b]	Droppings[a]	Birds[b]	Droppings[a]	Birds[b]
Male	443	24	339	26	172	24
Female	246	14	107	6	267	26
All (includes unsexed)	752	39	498	32	475	55
All.km^{-2}.survey^{-1}	853[c]	1.8[d]	699[c]	1.8[d]	570[c]	2.5[d]
Sample size[e]	11008	–	8905	–	10425	–

[a]total records, [b]total sightings excluding chicks and poults, [c]per km^2 of transect area, [d]per km^2 of study area, [e]grid locations × number of surveys.

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Table 2. Symbols.

Symbol	Definition
Pf	Probability of finding droppings
Pf_{max}	Vertex where Pf reaches (first) maximum
Pf_{min}	Vertex where Pf reaches (first) minimum
CL	95% confidence limits
dE	Distance (m) from grid location to nearest entrance or point of entrance zone
dT	Distance from grid location to nearest track
dT(0)	Point on track centreline
dT_{sig}	Value of dT at which the upper/lower CL equals Pf_{max} /Pf_{min} respectively
dT_{max}	Value of dT at Pf_{max}
Bc	Distance from bog centre
Be	Distance from nearest bog edge

Preliminary analysis showed the quantity of droppings at a location to be no more informative than their presence. We therefore used logistic (presence/absence) models: generalised linear mixed models (GLMMs) with binomial distribution, logit link, and corrected for any extra-dispersion. Transect-based survey was entered as a random effect and degrees of freedom were estimated with Satterthwaite's approximation. GLMMs were done with the SAS Glimmix macro (Littell et al. 1996, SAS ver. 9.1).

Temporal covariance among observations was possible because the same transects were walked on successive surveys and so the same droppings might have been recorded more than once. Spatial covariance was also likely if the frequency of droppings at adjacent locations was correlated. Appropriate covariance structures were therefore specified in GLMMs (Appendix 1).

Model specification

GLMMs with Pf as the response variable modelled the distribution of droppings at each study area. Our aim was to estimate parameter values for focal explanatory variables, as defined at the outset, and not to predict Pf. We first specified dT, and then defined track-use classes (Table 3) expecting Pf to be lower near more-used tracks. Maps (Fig. 2) showed droppings to be much sparser near woodland entrances and so models controlled for dE. Finally, the Anagach map showed obvious differences in Pf between dry and boggy ground and so here we defined a habitat category (dry/boggy). Additionally, the Anagach map showed greater Pf nearer centres of bigger bogs and so a distinct GLMM, for boggy ground only, described the distribution of Pf on bogs of different sizes in terms of Be and Bc.

We assumed nothing about the shape of the relationship between dT and Pf, addressing it in two stages. First, it was accurately portrayed by empirical models based on distance categories or 'bands' (e.g. 0–20 m, 20–40 m and so on). Band-based models, however, did not provide explicit relationships between dT and Pf, and were impracticable for studying interactions between dT and categorical variables (track-use class and habitat).

Polynomials in dT were more manageable and also represented the dT–Pf relationship empirically, each extra term giving a closer fit to data but wider confidence limits (CL). As the relationship was always non-linear, we began the model for each area with a quadratic polynomial and used AIC (Akaike's information criterion, SAS ver. 9.1) to judge whether an extra, cubic term was informative (Appendix 1: Model development). Terms higher than cubic did not improve AIC and so choices lay between quadratic and cubic. To check where on the trajectory any improvements had occurred, trajectories for quadratic, cubic and comparable band-based models were overlaid.

One way of controlling for dE was to use a polynomial, as for dT. We routinely used a cubic polynomial in dE, preferring this to a quadratic because it ensured a good fit to the data, CL width being immaterial. An option was to use the polynomial to discover how far dE impacted Pf (Fig. 4), and then drop all data within this distance (Boat of Garten 300 m, Anagach 400 m, Glenmore 800 m) plus the polynomial.

Models including track-use classes (Table 3) described two (Boat of Garten and Anagach) or three (Glenmore)

Table 3. Track-use classes, physical descriptions with width in m, and experts' disturbance rankings (1–6), ordered by Pf (Table 2).

Use class	Boat of Garten	Anagach	Glenmore
More	1. Improved track, 2 m 2. Overgrown track, 2 m	1. Improved path, 1–2 m	1. Tarmac public road 3. Much-used track/path, 1–2 m
Less	3. Unimproved path, 1 m 4. Desire line, <1 m	3. Unimproved path, 1 m 2. Unimproved path, 1–2 m	2. Heavily-used track, 2+ m 4. Moderately-used track, 2+ m 5. Less-used track/path, 1–2 m
Disused			6. Derelict track, 2 m

track – vehicle track; path – footpath; desire line – narrow unimproved footpath. In the text, 'track' covers all three.
Physical types are numbered 1–6 according to disturbance rankings based on local experts' experience of people taking recreation plus, at Glenmore only, forestry vehicles. The Glenmore experts subdivided both 'track, 2+ m' and 'track/path, 1–2 m' into two rankings, as shown. Types are ordered from top to bottom according to increasing Pf, as shown by the track-use terms from a main-effects GLMM for each area. These were as in Appendix 1 Table 7–9, except that the track-use category included 3–6 physical types instead of 2–3 classes.
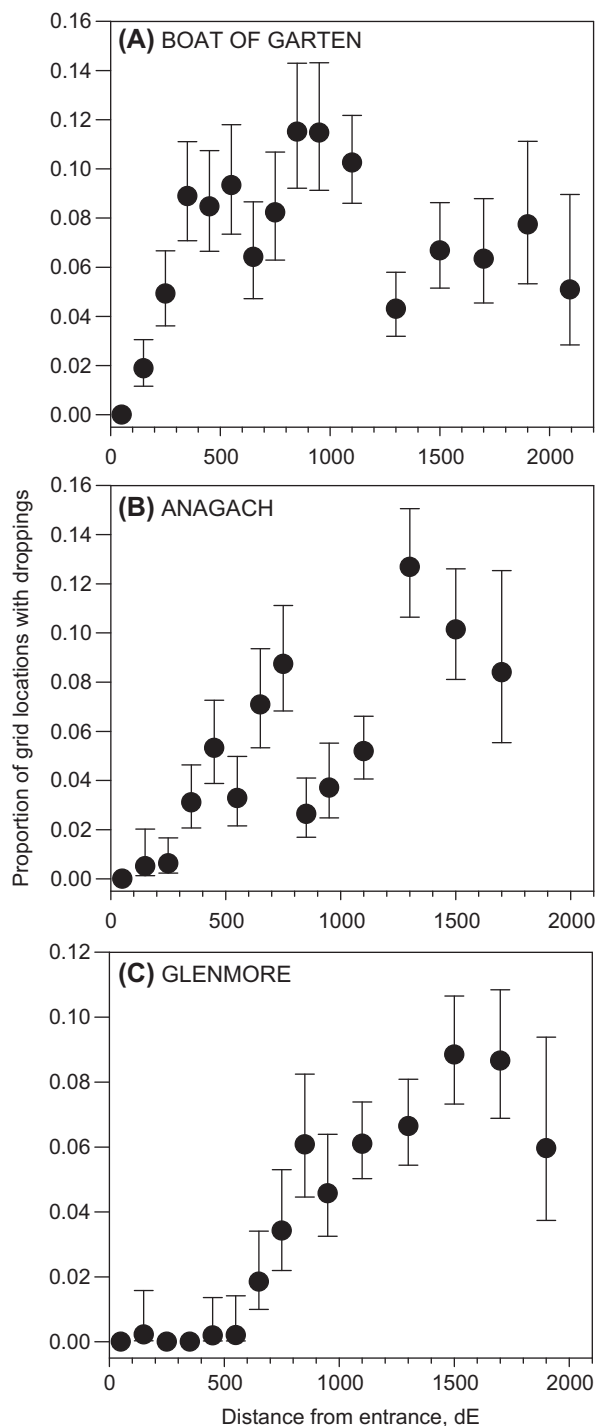
Figure 4. Proportion of grid locations with droppings vs distance from nearest entrance (m). Bars show 95% confidence limits from a logistic GLM using data from all surveys combined.

parallel trajectories for dT, these differing solely in intercept. At Anagach, adding the 'habitat' category gave four parallel trajectories. These were 'main-effects' models (Fig. 5).

In a uniform forest with track-use classes intermingled, however, trajectories should converge as they approach the value of dT at which Pf reaches its maximum (dT_{max}). Modelling this requires interactions between track-use class

and one or more parameters of the dT polynomial. We therefore checked for first-order interactions by backward selection. Starting with the interaction between track-use class and the highest polynomial term, we dropped insignificant ($p > 0.05$) interactions. No further term was dropped after a significant interaction was found. In effect, the shape of main-effects trajectories (Fig. 5) was an average, dissected into finer detail by interactions (Fig. 6).

An overall model for all three study areas together gave a simplified summary of how dT influenced Pf (Fig. 7). It controlled for dE by dropping grid locations close enough to entrances to be affected by them. For Glenmore, grid locations associated with disused track and more-used tracks (Table 3) were also dropped, the former because it was scarcely disturbed, the latter because only 31 observations of droppings were linked with them. As definitions of track-use classes differed among areas, these too were dropped. The model included the three study areas and habitat (dry/boggy ground at Anagach) as explanatory categories. A cubic polynomial described the effect of dT. This was checked for interactions with area and habitat as in the previous paragraph.

A distinct model described the distribution of Pf on the 12 boggy patches at Anagach. It included polynomials in dE and dT and, for each grid location on boggy ground, characterised bog size by Be + Bc (Appendix 1 Table 11). A quadratic term (Bc^2) represented uneven distribution of droppings between bog edge and bog centre. Graphical trajectories illustrating the effects of bog size on Pf were produced by applying parameter estimates for Be + Bc and Bc^2 to notional disc-shaped bogs. In addition, the benefits of bog size were illustrated as average Pf along a radius of a disc-shaped bog.

Model trajectories

Effects of dT on Pf were illustrated by using polynomial models to calculate 'probability trajectories' (Fig. 5) in which Pf increased with dT, from a minimum at dT(0) on the track centreline (y-intercept) to a maximum Pf_{max} at dT_{max}. The y-intercept for all models comprised the model intercept, plus the mean spatial covariance kernel (Appendix 1), the effects of dE at 1 km from the nearest entry point (Anagach and Glenmore) or zone (Boat of Garten), a track-use term and a habitat term (Anagach).

Trajectories were based on calculations of Pf at 10 m intervals conditional on an invariant value of Pf at dT(0). CLs at each distance were based on 10 000 model simulations: in each, for each parameter estimate, a value was taken at random from its normal distribution, as reconstituted from its mean and standard error. The 10 000 estimates of Pf were ranked, the 250th and 9750th being taken as 95% CL.

Increases in Pf were statistically significant up to the distance (dT_{sig}) at which the upper CL equalled Pf_{max} (see arrows in Fig. 5).

Trajectories differed in shape and average Pf. To compare shapes directly, each trajectory was scaled so that its average Pf was the same. For example, a trajectory calculated at 10 m intervals from 10–300 m, gave 30 estimated probabilities. Each was divided by their sum to give 30 scaled probabilities totalling 1.00.
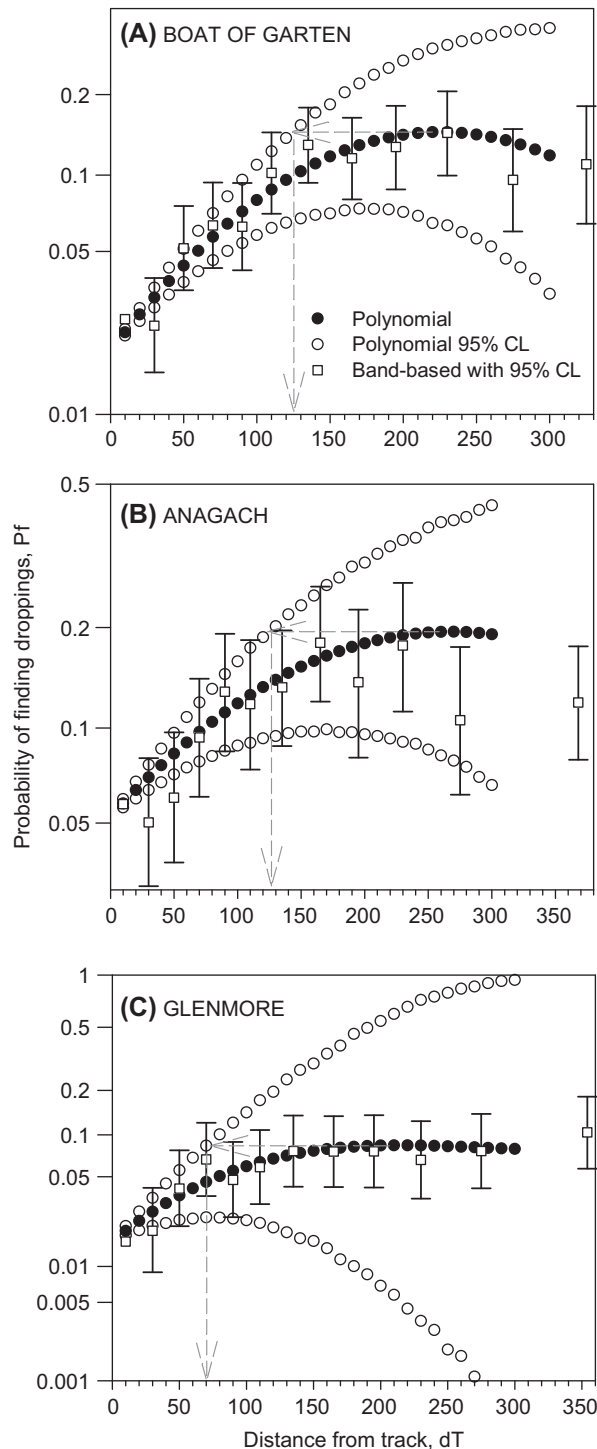
Figure 5. Probability trajectories (probability of finding droppings Pf versus distance from track dT) for comparable band-based and main-effects polynomial models, with 95% CL. The right-hand band is plotted at median dT for grid locations where $dT \geq 300$ m. Grey arrows lead from the polynomial vertex Pf_{max} to dT_{sig} (the value of dT at which the upper CL for $Pf = Pf_{max}$), which is the distance out to which the track effect was significant. Main-effects models had 2–4 parallel trajectories differing solely in intercept and so these comparisons are based on one trajectory per area.

Figure 6. Probability trajectories from models with interactions. Black symbol (grey for disused track at Glenmore) shows the distance dT_{sig} out to which the track effect was significant, to the nearest 10 m. Each trajectory stops at the vertex Pf_{max} or (for disused track) Pf_{min}.

Figure 7. Probability trajectories from overall model for all three study areas together. Contrasting symbol in each trajectory shows the distance dT$_{sig}$ out to which the track effect was significant, to the nearest 10 m.

Demography

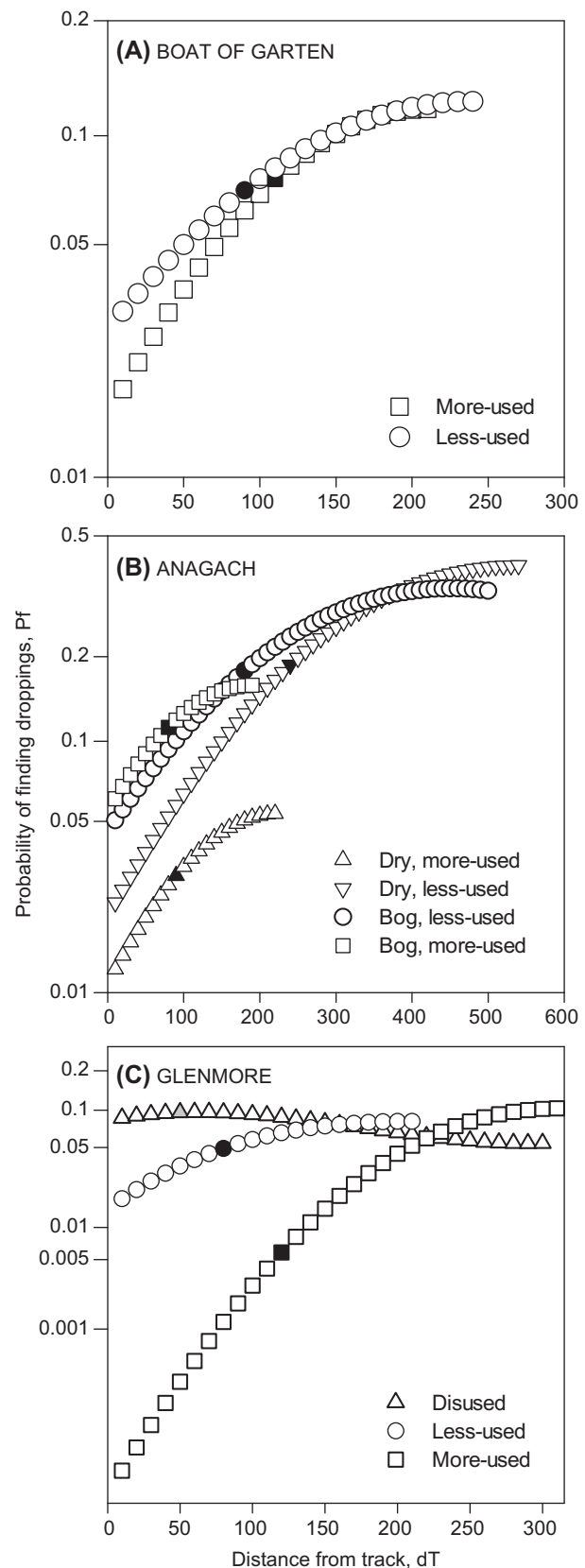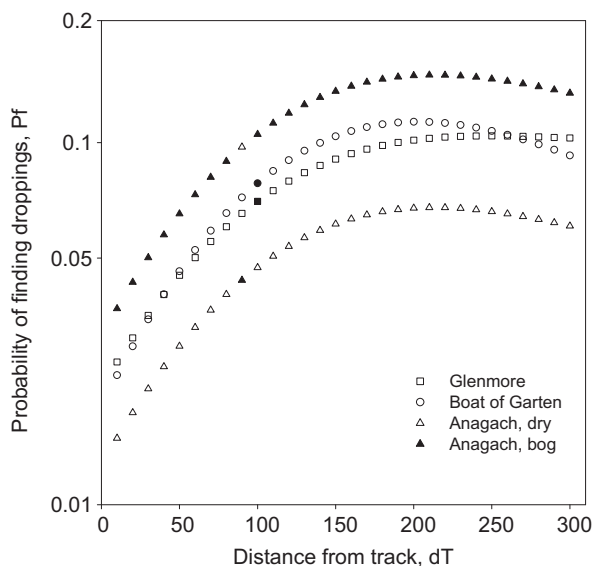The number of chicks or cocks per hen seen on brood counts during 2006–2011 was analysed using GLMMs with a Poisson distribution and log link, the natural logarithm of hen numbers as an offset, a generalised AR(1) covariance structure (Appendix 1) for the repeated parameter 'site', and corrected for any extra-dispersion. 'Year' was entered as a random effect. Each analysis had a single fixed effect that classified the 12 sites in different ways, such as more-disturbed versus less-disturbed.

We also assessed the number of cocks per hen from droppings at the three main study areas. This involved a GLMM with area as the fixed effect, Poisson distribution and log link, the natural logarithm of the number of observations of hens' droppings as an offset, and corrected for any extra-dispersion. The random effect 'survey' had a covariance parameter estimate ≤ 0 and so was dropped from the model, which reverted to a GLM (SAS ver. 9.1, Genmod procedure).

The mean number of capercaillie sightings per km of transect walked on dry versus boggy ground at Anagach was estimated from the numbers noted during each survey. This involved a GLM with Poisson distribution and log link, with the natural logarithm of the number of km walked on each ground type during each survey as an offset. The single fixed effect was ground type.

Assumptions and errors

We assume that Pf reflects use of ground by capercaillie. The persistence of droppings and the proportion missed by observers must, however, have varied with season, weather, terrain and vegetation. Also, vegetation structure, which we did not measure, must have influenced flushing distances (Thiel at al. 2007a) and bird distribution.

Furthermore, positions of tracks and droppings were subject to GPS and mapping errors. We perforce assumed that errors were effectively random.

Two measurements were based partly on expert judgement. First, track-use classes (Table 3) gave coherent results and any plausible errors in classification would have left the main conclusions unaffected. Second, the two independent rankings of disturbance for the 12 study sites agreed well (Kendall $r = 0.91$, p < 0.0001). There was perfect agreement on the four most disturbed: Anagach, Boat of Garten, Glenmore and part of Rothiemurchus estate being ranked 1, 2, 3 and 4 respectively (1 = most disturbed).

Brood counts were in largely open forest where dogs could be followed (Baines et al. 2011), so avoiding dense habitats used by moulting cocks. Hence counts might not represent the sex ratio in the Spey valley as a whole. Also, hens with and without broods might have used different habitats, so biasing estimates of reproductive rate. Finally, we did not measure the openness of study areas, although it might have influenced sex ratios and reproduction. We discuss this.

Results

Entrances and tracks

The effect of dE on Pf was large and obvious although its form was specific to each area (Fig. 2, 4). The impacts of dT on Pf, shown as probability trajectories (Fig. 5–8), varied with circumstances and evidently reflected differences in the birds' response to track-based disturbance. In particular, trajectories showed the distance out to which a track significantly impacted Pf (dT$_{sig}$) on each side.

At Boat of Garten, trajectories (Fig. 6) for more- and less-used tracks showed Pf starting at different values on and near tracks but reaching very similar ones (0.090 and 0.092) by 130 m. This was consistent with disturbance being greater near more-used tracks but similar sufficiently far from tracks.

At Anagach, there were two categorical variables (track-use and habitat) and hence four trajectories (Fig. 6). Close to tracks, and irrespective of track-use class, Pf was lower on dry than on boggy ground. This was consistent with birds on boggy ground being less disturbed by people and dogs.

In addition, on dry ground near tracks, Pf for more-used tracks was lower than for less-used ones, consistent with more-used tracks causing more disturbance. But on boggy ground near tracks the difference in Pf between track-use classes was negligible, showing that an increase in track use caused little extra disturbance of birds on boggy ground.

More surprisingly, on both ground types, dT$_{sig}$ for less-used tracks (180 or 235 m, Table 4) was much greater than for more-used ones (75 or 90 m) and Pf$_{max}$ was quite similar for both less-used trajectories (Fig. 6). This was explained by the spatial layout of tracks and bogs (Fig. 2). Thus the easternmost bog had less-used tracks to its north and west but none to its south or east. It supported high values of Pf, as did dry ground just to its south – a secluded area relatively well-removed from track-based disturbance and partly sheltered from it by the bog. Hence

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Table 4. Impact of tracks on droppings: distances out to which tracks depressed Pf, according to specified models, rounded to 5 m.

| Study area | Main-effects model All tracks | | | Main effects plus interactions | | | | | |
| | | | | More-used tracks | | | Less-used tracks | | |
	dT_{sig}[a]	dT_{max}[b]	Model[c]	dT_{sig}	dT_{max}	Model	dT_{sig}	dT_{max}	Model
Boat of Garten	125	230	B1	110	210	B2	90	240	B2
Anagach dry	125	270	A1	90	220	A2	235	540	A2
Anagach bog	125	270	A1	75	190	A2	180	450	A2
Glenmore	70	215	G1	115	310	G2	75	215	G2

[a]distance of significant impact, [b]distance to maximum Pf, [c]see Appendix 1.

Fig. 6 portrayed what was on the ground, although the underlying model (A2, Appendix 1 Table 8) was inexplicit about the spatial mechanism.

At Glenmore, Pf was strikingly low near more-used tracks (Fig. 6). These were mostly footpaths near entrances, many heavily used by people going off-track for activities such as picnicking and exercising dogs. Accordingly, such tracks had few (31) observations of droppings associated with them and for all these $dT \geq 158$ m. Hence dT_{sig} (115 m, Table 4) was probably underestimated due to low sample size and wide CL. Pf was high near the disused section of track (Fig. 6), even declining with increasing dT. This natural experiment therefore showed no evidence of associated disturbance, as predicted.

The overall model (Fig. 7, Appendix 1 Table 10) included significant interactions between the area category and two parameters of the track polynomial, so confirming that trajectories from the three study areas differed in shape. Whereas dry ground at the most-disturbed area, Anagach, had the lowest frequency of droppings, boggy ground had the highest. Nonetheless, dT_{sig} was similar (90–100 m) at all three study areas.

Cocks and hens

The distance at which a capercaillie flies when disturbed by a walker, its 'flushing distance', typically averages about 30 m but is greater for cocks than hens (Catt et al. 1998, Thiel et al. 2007a). Accordingly, scaled trajectories for cocks and hens at Boat of Garten and Glenmore showed more hens' droppings closer to tracks (Fig. 8).

Distinguishing cocks' from hens' droppings (Appendix 1) may well have involved some misclassifications. Nonetheless, cock to hen ratios in droppings (Table 1) were similar to ratios in bird sightings (Table 5), so supporting the distinction on a population basis. This does not imply that all assignments were correct. If not, differences between cocks and hens (Fig. 8) are probably underestimated.

Data for Anagach hens were too few for a separate model. The sex ratio from droppings there, however, did not differ between dry and boggy ground (Table 5, footnote b).

Bogs at Anagach

Overall, Pf was higher on boggy than on dry ground (Fig. 2, 6, 7). Perhaps droppings were easier to detect on bogs. Against this explanation, there were 0.34 (CL 0.20–0.58) sightings of capercaillie per km of transect walked on boggy ground and

only 0.14 (CL 0.09–0.22) on dry (difference: $\chi^2_{1,8} = 6.16$, p = 0.013). The boggy/dry ratio from these sightings (2.4) is very similar to that based on Pf (2.2 for the two Anagach trajectories in Fig. 7). Also, Pf was similar on both boggy and dry ground far from track-based disturbance (Fig. 2), Pf_{max} reaching 0.34 for boggy ground and 0.40 for dry (Fig. 6). All this is consistent with birds using most dry ground less, due to greater disturbance there, but making similar use of both types of ground where each was tranquil enough.

Model A3 (Appendix 1 Table 11) represents the observations (Fig. 2) that droppings were seen more frequently on
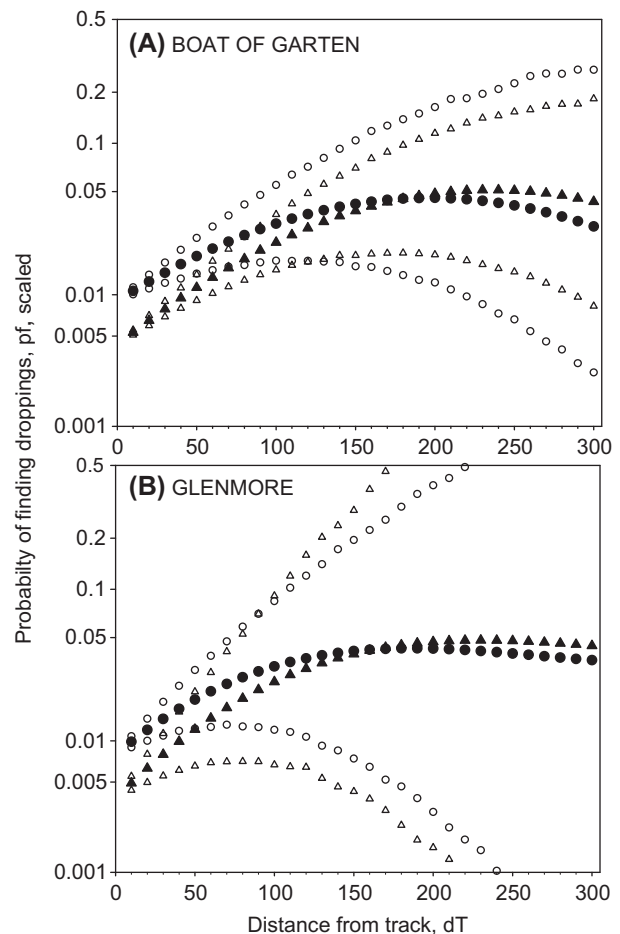

Figure 8. Comparable (scaled) probability trajectories for cocks (▲) and hens (●) with 95% CL (Δ, ○) at Boat of Garten and Glenmore. From main-effects models.

Table 5. Demographic measurements from main study areas and other parts of the Spey valley, 2006–2011.

Site	Hens Total	Chicks per hen From counts		Cocks per hen From counts		From droppings	
		Mean	95% CL	Mean	95% CL	Mean	95% CL
Anagach	8	0.85	0.17–4.2	3.78	1.51–9.5	3.17[b]	2.12–4.7
Boat of Garten	12	1.08	0.24–4.8	1.23	0.36–4.2	1.80	1.27–2.6
Glenmore (in)[a]	32	0.89	0.32–2.5	0.51	0.14–1.8	0.64	0.37–1.1
Glenmore (out)[a]	59	1.19	0.51–2.8	0.94	0.46–1.9	–	–
Other (9 sites)	395	0.65	0.31–1.4	0.76	0.53–1.1	–	–

[a] inside and immediately outside study area (Fig. 2) respectively, [b] boggy ground 3.76 (CL 2.01–7.0), dry ground 3.03 (CL 1.59–5.8), $\chi^2_{1,3.27} = 0.52$, p = 0.52.
Covariance parameter estimates for respective random effects 0.39 (CL 0.13–4.49), 0.030 (CL 0.005–1789), ≤ 0 (so effect dropped).

bigger bogs, and closer to bog centres. After controlling for dE and dT, a bigger bog supported higher values of Pf, which increased towards its centre (Fig. 9).

The benefits of bog size increased more or less linearly with bog radius (Fig. 10) within the observed range of bog size (maximum radius ~200 m). Extrapolation well beyond this suggested that benefits would stop increasing at a radius of ~600 m (~1 km^2). This result remains to be substantiated beyond ~200 m.

Demography

The number of cocks per hen was much biased towards cocks at Anagach and to a lesser extent at Boat of Garten, but it was the other way round at Glenmore and the other nine Spey valley sites combined (Table 1, 5). Results from droppings found during surveys, and birds seen during brood counts, agreed well.

The number of chicks reared per hen was no less at our three main study areas than at the other nine, which were all ranked as less disturbed (Table 5). If anything, it was slightly

more ($F_{1,17.1} = 3.19$, p = 0.092). Indeed, a comparison between the four most disturbed sites (chicks per hen 0.99, CL 0.48–2.02) and the other 8 (0.63, CL 0.31–1.27) showed a significant difference ($F_{1,18.8} = 4.67$, p = 0.044).

Discussion

Entrance effects

Effects of entrances on Pf (Fig. 2, 4) were striking but specific to each area. In itself, dE was plainly less important than correlates such as the number of people, their activities, the density of tracks, and (at Glenmore) elevation. Nonetheless, disturbance obviously deterred capercaillie from much ground near entrances. Similar effects probably impact entire woods near certain settlements. Some such woods have apparently good habitat but only occasional records of birds, some have records of birds being more abundant in the past. Just as Thiel et al. (2008) showed that capercaillie in central Europe avoided areas

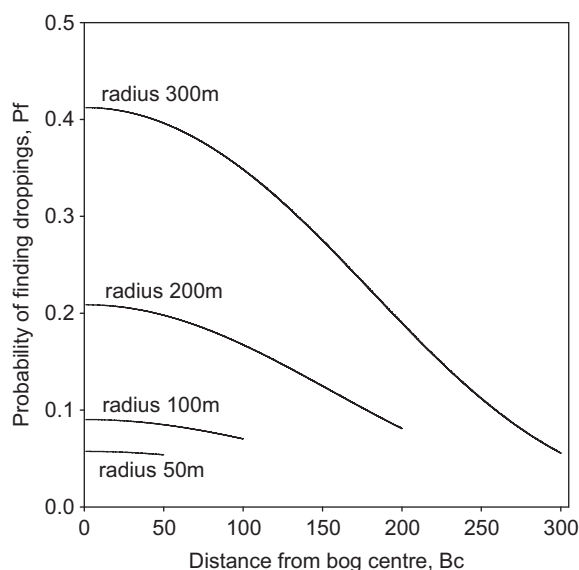Figure 9. Schematic effects of bog size on the probability of finding droppings (Pf). Calculated from empirical parameters in model A3 (Appendix 1 Table 11) as if Be and Bc lie on the radius of a disc-shaped bog.
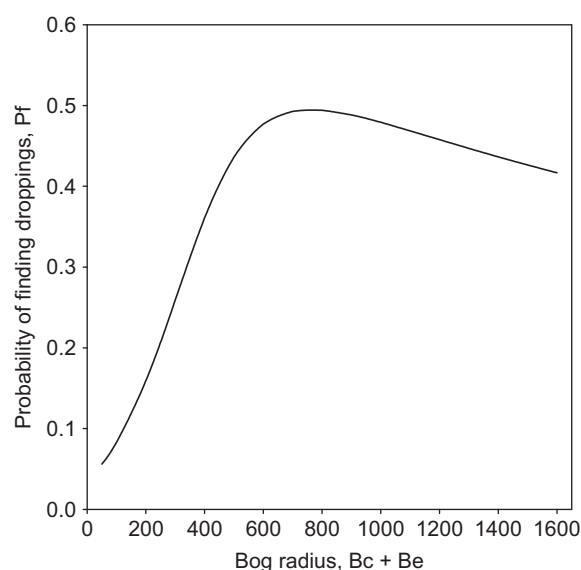

Figure 10. Schematic benefits of bog size, defined as the average probability of finding droppings (Pf) along the radius of a disc-shaped bog. Extrapolated from observed parameters in model A3 (Appendix 1 Table 11).

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highly disturbed by recreation, so we infer that fewer capercaillie now use such woods partly because of increased disturbance.

Track effects

Summers et al. (2007) studied vehicle tracks at Glenmore and Abernethy forests (near Boat of Garten, Fig. 1), using droppings under trees to measure ground use by capercaillie. They fitted a 'biologically plausible' model, in which tree use increased asymptotically with dT, but did not provide an equivalent of dT_{sig}. Of our trajectories, that for less-used tracks at Glenmore (Fig. 5, 6, 7) most resembles their model.

Alternatively, Patthey et al. (2012) used a linear trajectory to describe black grouse *Tetrao tetrix* hens with chicks avoiding 'roads, forest tracks and walking paths'. This implies that birds prefer to use the most remote parts of a disturbed area. Of our trajectories, the two for less-used tracks at Anagach (Fig. 6) increased continuously for much of their length and so came closest to this model. In these cases, dT_{sig} for less-used tracks was 180 or 235 m (Table 4) and only 10–15% of the ground lay more than 180–235 m from tracks (Fig. 3).

The trajectory at Boat of Garten (Fig. 5, 7, Appendix1: Model development) showed a third shape, peaking at 230 m and then declining. Birds disturbed near tracks move farther into woodland. They may stop short of the most remote woodland, giving rise to just such a peak.

Capercaillie disturbed by an off-track walker flush at a mean distance of ~30 m, with a mode at ~20 m, and >90% of flushing events <50 m with very few >70 m (Thiel et al. 2007a). Probability trajectories for less-used tracks at Glenmore and for locations on boggy ground near more-used tracks at Anagach (dT_{sig} 75 m in both cases, Table 4) agreed quite well with these flushing distances, as would be expected if people and dogs kept mostly to tracks. Other tracks seemed to cause disturbance to greater distances, probably because people and dogs regularly strayed off them.

Summers et al. (2007) indicated that disturbance associated with vehicle tracks effectively caused capercaillie to avoid 21–41% of woodland at Glenmore and Abernethy. Our data (Fig. 3, 6, Table 4) are not directly comparable with theirs but show that 50–60% of the ground at each area was within 75 m (dT_{sig} for less-used tracks at Glenmore) of a track and about 90% within 235 m (dT_{sig} for locations on dry ground far from the nearest, less-used, tracks at Anagach). Were it not for the relatively safe refuge provided by bogs at Anagach, there would probably be many fewer birds there (Fig. 2, 7). Entrance effects (Fig. 4) further increased the amount of ground affected.

Demography

Vital rates

Thiel et al. (2011) reasoned that elevated levels of the stress hormone corticosterone in disturbed capercaillie could impact fitness. Brenot et al. (1996), however, found no effect of disturbance on reproductive rate at a ski station in France. We also found no negative impact of disturbance on reproduction, despite anecdotal examples of capercaillie hens deserting disturbed nests and dogs killing chicks.

If anything, a capercaillie hen in a more-disturbed wood reared more chicks. Perhaps recreationists prefer woods with better brood habitat, such that disturbance and reproduction both reflect habitat. Or, disturbance might deter predators, so reducing predation on capercaillie broods. Thus, in Norway Wegge and Rolstad (2011) found that a capercaillie hen in perturbed commercial forest reared more chicks than in semi-natural old forest. They attributed this to fewer red foxes *Vulpes vulpes* in perturbed forest. Again, in boreal Russia reproductive rates of capercaillie, black grouse and hazel grouse *Bonasa bonasia* in forest perturbed by logging and hunting were generally higher than in unperturbed, native forest (Borchtchevski et al. 2003). In this case, however, there were more red foxes in the perturbed forest.

Red foxes show varied responses to buildings, a reasonable surrogate for disturbance. Thus, they avoided recreational cabins in Norway (Støen et al. 2010) and settlements in Switzerland (Weber and Meia 1996), but spent much of their time around houses in rural Japan (Cavallini 1992).

Furthermore, corvids were attracted to mountain huts in Bavaria (Storch and Leidenberger 2003) and to recreational cabins in Norway, near which reproduction of willow ptarmigan *Lagopus lagopus* was depressed (Støen et al. 2010). Similarly, food scraps left by tourists attracted corvids to Scottish ski slopes, where they took eggs and chicks of rock ptarmigan *Lagopus muta* (Watson and Moss 2004).

All this highlights the difficulty of interpreting the impact of recreational and other disturbance on vital rates in complex situations already perturbed by forestry. There is little evidence concerning impacts of disturbance on adult survival rate, apart from the suggestion that movement due to disturbance might increase mortality from collisions with forest fences.

Cocks and hens

The evidence on whether cocks or hens are more affected by disturbance seems conflicting. Cocks may be more readily disturbed by walkers. Thus, flushing distances are greater for cocks than hens (Catt et al. 1998, Thiel et al. 2007a), and Pf near tracks was less for cocks than for hens (Fig. 8). Contrary evidence suggests that hens are more susceptible to disturbance: albeit a different species, hen sharp-tailed grouse *Tympanuchus phasianellus* ceased to attend experimentally disturbed leks while cocks continued to display (Baydack and Hein 1987). Similarly, there were fewer hens than cocks at Anagach and Boat of Garten (Table 5), the two most disturbed of our 12 study sites. Finally, some evidence from Anagach suggests no difference between the sexes: bogs acted as refuges, where one would expect to find proportionally more droppings from the more easily-disturbed sex. But there was no evidence of this (Table 5, footnote b).

Perhaps something about Anagach and Boat of Garten, unrelated to disturbance, deterred hens. For example, habitat preferences differ between sexes, hens preferring denser vegetation (Thiel et al. 2007b). We cannot rule this out. Nonetheless, disturbance might cause a lack of hens, as follows.

Irrespective of disturbance, natal dispersal distances are greater for hens than cocks (Moss et al. 2006). Hence, on the

scale of our study areas, most cocks are locally recruited whereas many young hens leave their natal area, the sex ratio being restored by immigrants. Chicks reared in disturbed woodland may adapt somewhat to disturbance, but those raised in tranquillity may not. Thus, young cocks may remain on disturbed ground, while young hens from less disturbed woodland may be deterred from settling, so unbalancing the sex ratio against them. Brenot et al. (1996) also attributed the decline of capercaillie at a ski station to failing recruitment, but recorded no difference between sexes.

The hypothesis that recreational disturbance causes unbalanced sex ratios is open to experiment. The proportion of hens at Anagach and Boat of Garten should increase if disturbance there lessens. Also, at areas with more balanced (Table 5) sex ratios, the proportion of hens should decline if disturbance increases.

Population consequences

Whatever the reasons, cocks at Anagach or Boat of Garten had fewer hens around them. They may therefore have been less likely to procreate than cocks in quieter woods, increasing the probability of their genes being lost to the small Scottish population. In turn, this could augment the likelihood of inbreeding depression and consequent extinction (Moss et al. 2003). This could be further hastened if some lost genes imparted resilience to disturbance.

Disturbance did not seem to depress the hens' reproductive rate but it did deny birds territory. Having moved elsewhere, birds may reproduce and survive just as well unless inbreeding depression (previous paragraph) or density dependence (Gill et al. 2001) impact fitness. Density-dependent effects may seem unlikely at current low densities (Ewing et al. 2012), however, and disturbance may redistribute birds without depressing their vital rates.

To the contrary, metapopulations in fragmented habitat, such as Scottish capercaillie (Watson and Moss 2008), may benefit from more, bigger and closer habitat fragments irrespective of bird density. If so, by reducing the effective number and size of useable woodland fragments, disturbance could make this fragile population more liable to extinction.

Refuges

Refuge size

Although the value of a grouse refuge depends partly upon topography and cover (Brøseth and Pedersen 2010), area is a prime consideration. Romanov (1979) suggested that, to avoid over-hunting, refuges for capercaillie in boreal Russia should be 9 km^2 of unlogged native habitat. An expert group on grouse suggested no disturbance within 1 km of lekking places and brood habitats (Suchant and Braunisch 2004), implying refuges of at least 3 km^2. Braunisch and Patthey (2011) recommended refuges for black grouse disturbed by snow sports but did not propose a minimum size. Zeitler (2007), however, suggested that strictly protected areas of $\geq$ 30–50 ha might allow black grouse populations to persist in much-disturbed areas.

Bogs at Anagach acted as refuges but did not sustain a normal sex ratio. At Boat of Garten too there was a dearth of hens, suggesting that ground between tracks was not tranquil enough to support the usual proportion of hens.

At both woods, people and dogs roamed off tracks, such that even the Anagach bogs were somewhat disturbed.

At Glenmore, disturbance in the north and east of the study area obviously deterred capercaillie (Fig. 2), while birds in remoter parts showed a reproductive rate and sex ratio similar to that in other parts of the Spey valley (Table 5). Ground adjacent to less-used tracks at Glenmore was rougher and more difficult underfoot than at Anagach or Boat of Garten, and dT_{sig} (75 m) was consistent with walkers flushing birds without leaving tracks. The three most southerly blocks of ground, delineated by used tracks or the edge of the study area (Fig. 2), were well-used by capercaillie and ranged from 53–90 ha, although only the 53 ha one was completely surrounded by tracks.

The Glenmore example shows that Scottish woods with sufficiently large trackless compartments can sustain capercaillie if people and dogs keep largely to tracks, and that these can be smaller than the 3 km^2 indicated by Suchant and Braunisch (2004). The Glenmore compartments, however, lay next to each other and tracks between them were not in continuous use. How far apart different compartments can be before birds commute less between them, so that they are less useful to a population, is unknown. Our data are therefore insufficient to support a precise minimum refuge area, which in any case would be modified by resources such as cover and distances between refuges. With these caveats, the precautionary principle, current practice at Glenmore and Fig. 10 in mind, we nonetheless suggest 1 km^2 as a working minimum in Scotland.

Several compartments $\geq$ 1 km^2 would be required to sustain a single lekking population, which occupies 5–15 km^2 of woodland habitat (Watson and Moss 2008). An isolated lekking population, however, would become extinct through mishaps or enfeebled by inbreeding (Moss et al. 2003). Hence, management for capercaillie should be on the scale of entire watersheds (Watson and Moss 2008).

Track management

Kangas et al. (2010) showed that quite small numbers of hikers on marked trails had negative impacts on some forest bird species. Animals, however, are generally less disturbed by predictable activities (MacArthur et al. 1982, Knight and Cole 1995, Lenth et al. 2008), habituating to people and dogs that stay on tracks (Whittaker and Knight 1999, Miller et al. 2001, Wolf and Croft 2010). Less-disturbed parts of Glenmore supported normal sex ratios and reproduction in capercaillie (Table 5) despite some disturbance off used tracks. Presumably there is a threshold above which the frequency and nature of disturbing activities begins to impact populations. If so, this has yet to be measured.

Meanwhile, keeping people and dogs on tracks and track closure could benefit capercaillie by increasing the effective size of trackless compartments that serve as refuges. Our observation that the disused track at Glenmore (Fig. 2, 6) had unusually high Pf on and close to it, however, cautions against obliterating closed tracks. Borchtchevski (2009) recommended closing tracks in northwestern Russian taiga, but not destroying them because they provide preferred foods for hens in spring. In Scottish conditions, little-used tracks also provide grit, dust baths, drinking puddles, trees

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with thick branches favoured for roosting, display sites, and places to dry out after rain (Watson and Moss 2008).

Conclusions

Droppings proved an inexpensive way of mapping the distribution of capercaillie at a usefully fine-grained resolution. Disturbance within a few hundred metres of woodland entrances was so great that ground there was little used by capercaillie. Beyond this, disturbance associated with tracks deterred capercaillie from a belt of ground at least 140 m wide ($2 \times dT_{sig}$), up to 470 m where people and dogs strayed off tracks.

Management for capercaillie in Scotland should be on the scale of entire watersheds, comprising numerous refuges. Low track density and a culture that encourages people and dogs to stay on tracks could sustain more effective refuges. Off-track activities such as snowshoeing and orienteering are likely to be counterproductive. Hence management of such sports should be included in conservation plans based on refuges. Our results confirm that closing tracks, making ground near remaining tracks difficult underfoot, and rewetting ground previously drained for silviculture (SNH 2002) could each contribute to capercaillie management.

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Appendix 1

Classifying droppings

The number of intestinal droppings was recorded in four categories: <5, <20, <100, $100+$. Their apparent age was 'fresh' (greenish–yellow throughout with no fading of surface colour due to weathering, 'old' (weathered), or 'ancient' (weathered and losing shape). Classification by sex (male, female or uncertain) relied largely on diameter and the coarseness of undigested fibre. Amounts in each age or sex category were ranked. Clocker, chick and caecal droppings (amount indexed from 1–3, ascending) were noted separately. Of these characteristics, only presence and sex were used in statistical analyses, but all were useful for identifying repeat observations.

Repeated transects

Each of the 18 surveys was done by one of six observers, except for two at Glenmore where two observers each covered part of the ground. Separately, some transects were walked twice on the same day to assess how often records were repeated. To allow for potential GPS errors, pairs of records within 30 m of each other on the two transect walks were evaluated using the characteristics in the previous section.

On 6 May 2009, at Boat of Garten, the same observer walked the same transect twice. She recorded droppings eight times on each occasion, with one repeat. On 19 March 2009, at Glenmore, two observers each surveyed the same four transects. One observer recorded capercaillie droppings 23 times, the other 15. The latter, however, noted more droppings on one transect. Only one record was repeated exactly, plus two ambiguous ones with identical quantity, sex and age characteristics but separated by 30 m.

The results are what would be expected given that it was impossible to walk exactly the same route twice. The likelihood of recording the same droppings in successive surveys, and so inflating temporal covariance in Pf was evidently low. We nonetheless allow for it in models.

Modelling covariance

Temporal covariance was modelled (via the SAS ver. 9.1 Repeated statement) using a generalized AR(1) structure that applied to unequal intervals between observations (spatial power law). This measured the covariance between two observations at times t1 and t2 (median date of each transect-based survey) as $cov(y_{t1} + y_{t2}) = \sigma^2 \rho^{|t1-t2|}$ where ρ is an autoregressive parameter that satisfies $|\rho| < 1$ and σ^2 is an overall variance.

Preliminary analysis showed that the occurrence of droppings was correlated between grid points up to 80 m apart, the strength of correlation being similar up to 80 m and then falling sharply. Therefore, spatial covariance was modelled by means of a variable ('kernel') comprising the average frequency of sign at locations ≤ 80 m from the focal location. There were usually eight such nearby locations, but fewer (minimum four) close to the boundary of a study area.

When calculating polynomial trajectories, the kernel was included in the intercept as the parameter estimate multiplied by the mean.

Model development

Much variation in Pf remained unexplained by models, such that AIC values initially increased as a cubic polynomial controlling for dE, track-use classes and a quadratic in dT, plus the habitat category at Anagach, were included (Appendix 1 Table 6). This was acceptable because models were used to estimate parameters for these effects, not to predict Pf. Nonetheless, we had to decide whether adding a cubic term to each dT quadratic was informative, and used AIC to do this.

For Boat of Garten and Anagach, AIC increased with a cubic term (ΔAIC 249 and 599 respectively), but for Glenmore it declined (ΔAIC –194). This suggested a quadratic polynomial to describe the effect of dT on Pf at Boat of Garten and Anagach, and a cubic one at Glenmore. We checked this visually by overlaying comparable band-based, quadratic and cubic model trajectories (Appendix 1 Fig. 11).

Quadratic polynomials are often used to fit n-shaped curves. Accordingly, band-based models for Boat of Garten and Anagach (Fig. 5) both showed Pf falling when $dT > 230$ m (locations in the 210–250 m band vs those beyond 250 m gave $t_{6492} = 2.07$, $p = 0.039$ and $t_{3989} = 2.22$, $p = 0.026$, respectively). At Glenmore, by contrast, there was an insignificant uptick for $dT > 230$ m ($t_{4229} = 1.43$, $p = 0.15$).

The main difference between band-based and comparable polynomial models was within 60 m of tracks (Fig. 5). According to band-based models Pf remained low within 30 m (band 20–40 m) of dT(0) at Boat of Garten and Glenmore, and 50 m (40–60 m) at Anagach; but polynomials showed an immediate increase in Pf with dT. Otherwise, the two types of model agreed well.

At the outset we classified tracks into 3–6 physical types per area, reducing them to 2–3 use classes (Table 3). The effect of each initial type on Pf, estimated from models, agreed well with local experts' disturbance rankings – with

Table 6. AIC (first line) and ΔAIC (other lines) for successively added parameters of main-effects models (Appendix 1 Table 7–9).

	Study area		
Parameter	Boat of Garten	Anagach	Glenmore
Intercept only	62 971	51 663	62 343
Kernel[ab]	461	3036	726
Entrance cubic[a]	684	751	7685
Track quadratic[ac]	1724	1510	1157
Habitat[a]	–	599	–
Track cubic	249	599	−194

[a]ΔAIC not considered during model specification, [b]spatial covariance kernel, Appendix 1, [c]plus track use-classes as appropriate (Appendix 1 Table 7–9).

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Table 7. Boat of Garten model parameter estimates.

Parameter	Model B1				Model B2[a]			
	Estimate	SE	DF	P(t)	Estimate	SE	DF	P(t)
Intercept	−5.628	0.346	51	0.0001	−3.54	0.290	33.8	0.0001
Kernel	1.170	0.293	10^4	0.0001	1.328	0.311	7785	0.0001
Entrance	0.00668	0.000860	7393	0.0001	–	–	–	–
Entrance^2	−0.00653	0.000856	7376	0.0001	–	–	–	–
Entrance^3	0.00183	0.000257	7358	0.0001	–	–	–	–
Less	0	–	–	–	0	–	–	–
More	−0.369	0.140	7375	0.008	−0.618	0.266	5576	0.020
Track	0.0192	0.00167	7555	0.0001	0.0132	0.00278	5574	0.0001
Track^2	−0.0426	0.00522	7375	0.0001	−0.0276	0.00803	5470	0.0006
Track × **Less**	–	–	–	–	0	0	0	0
Track × **More**	–	–	–	–	0.00728	0.00355	5516	0.040
Track² × **Less**	–	–	–	–	0	0	0	0
Track² × **More**	–	–	–	–	−0.0213	0.0109	5490	0.0495

Entrance and Track units are m, Entrance^2 and Track^2 units are m × 10^3, Entrance^3 units are m × 10^6. Track-use classes (less-used, more-used) in bold. SE standard error of estimate. DF degrees of freedom. P(t) probability of greater t-value. Covariance parameter estimates for random effect survey: model B1 0.34 (CL 0.14–1.53), model B2 0.29 (0.12–1.34).
[a]excluding data < 300 m from entry zone to control for entry effect. With full data, interactions between track-use class and track quadratic were insignificant, possibly due to anomalies near entry zone (Fig. 2).

Table 8. Anagach models A1 and A2 parameter estimates.

Parameter	Model A1				Model A2			
	Estimate	SE	DF	P(t)	Estimate	SE	DF	P(t)
Intercept	−5.716	0.646	137	0.0001	−7.053	0.693	186	0.0001
Kernel	3.500	0.254	5501	0.0001	3.161	0.263	5644	0.0001
Entrance	0.00690	0.00213	3556	0.0012	0.00432	0.00226	3603	0.056
Entrance^2	−0.00571	0.00238	3558	0.0164	−0.00128	0.00260	3611	0.62
Entrance^3	0.00143	0.00081	3558	0.078	−0.00067	0.00093	3618	0.47
Dry	−0.951	0.117	3570	0.0005	0	–	–	–
Bog	0	–	–	–	1.654	0.244	3624	0.0001
Less	0	–	–	–	0.667	0.301	3597	0.027
More	−0.451	0.129	3624	0.0001	0	–	–	–
Track	0.0110	0.00167	3602	0.0001	0.0146	0.00315	3595	0.0001
Track^2	–0.0205	0.00375	3588	0.0001	−0.0326	0.00782	3585	0.0001
Track × **Less**	–	–	–	–	−0.00193	0.00377	3601	0.61
Track × **More**	–	–	–	–	0	–	–	–
Track × **Dry**	–	–	–	–	0	–	–	–
Track × **Bog**	–	–	–	–	−0.00217	0.00094	3643	0.022
Track^2 × **Less**	–	–	–	–	−0.0210	0.00908	3584	0.021
Track^2 × **More**	–	–	–	–	0	–	–	–
Dry × **Less**	–	–	–	–	0	–	–	–
Dry × **More**	–	–	–	–	0	–	–	–
Bog × **Less**	–	–	–	–	−0.657	0.237	3605	0.0056
Bog × **More**	–	–	–	–	0	–	–	–

Conventions as in Table 7. Track-use and habitat classes in bold. Covariance parameter estimates for random effect survey: model A1 0.34 (CL 0.12–3.15); model A2 0.33 (CL 0.12–3.10).

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Table 9. Glenmore model parameter estimates.

Parameter	Model G1[a]				Model G2[b]			
	Estimate	SE	DF	P(t)	Estimate	SE	DF	P(t)
Intercept	−10.830	1.920	3153	0.0001	−8.012	1.392	5765	0.0001
Kernel	2.506	0.442	7532	0.0001	2.377	0.354	10^4	0.0001
Entrance	0.0134	0.00546	3180	0.014	0.00993	0.00367	5892	0.0069
Entrance^2	−0.00866	0.00496	3191	0.081	−0.00523	0.00329	5901	0.11
Entrance^3	0.00187	0.00144	3204	0.20	0.0800	0.00094	5916	0.40
More	–	–	–	–	−8.851	1.872	5903	0.0001
Less	–	–	–	–	−1.793	0.422	5795	0.0001
Disused	–	–	–	–	0	–	–	–
Track	0.0205	0.00440	3245	0.0001	0.00589	0.0061	5770	0.33
Track^2	−0.0782	0.0234	3232	0.0009	−0.569	0.0227	5855	0.012
Track^3	0.0946	0.0361	3228	0.0009	0.107	0.0289	5913	0.0002
Track $\times$ **More**	–	–	–	–	0.0628	0.0152	5907	0.0001
Track $\times$ **Less**	–	–	–	–	0.0157	0.00619	5793	0.011
Track $\times$ **Disused**	–	–	–	–	0	–	–	–
Track$^2 \times$ **More**	–	–	–	–	−0.103	0.0310	5925	0.0009
Track$^2 \times$ **Less**	–	–	–	–	−0.281	0.0184	5868	0.13
Track$^2 \times$ **Disused**	–	–	–	–	0	–	–	–

[a]based on grid locations nearest to less-used tracks only, because more-used tracks had only 31 observations of droppings associated with them, [b]based on all data.
Conventions as in Table 7. Covariance parameter estimates for random effect survey: model G1 0.043 (CL 0.012–1.18); model G2 0.029 (CL 0.008–0.92).

Table 10. Overall model parameter estimates.

Parameter	Estimate	SE	F[a]	DF	P(F)
Intercept	−4.012	0.262	–	–	–
Kernel	2.801	0.173	509.7	1,784	0.0001
Bog	0.859	0.108	5.00	1,17.3	0.039
Area A	−0.506	0.342	3.84	1,15.8	0.044
Area B	−0.138	0.319	–	–	–
Area G	0	–	–	–	–
Track	0.0178	0.0265	124.5	$1,2 \times 10^4$	0.0001
Track $\times$ **Area A**	0.00164	0.00234	5.81	$2,2 \times 10^4$	0.0030
Track $\times$ **Area B**	0.00357	0.00249	–	–	–
Track $\times$ **Area G**	0	–	–	–	–
Track^2	−0.0632	0.0123	85.7	$1,2 \times 10^4$	0.0001
Track$^2 \times$ **Area A**	−0.00596	0.00549	5.30	$2,2 \times 10^4$	0.0050
Track$^2 \times$ **Area B**	−0.0118	0.00690	–	–	–
Track$^2 \times$ **Area C**	0	–	–	–	–
Track^3	0.0734	0.0178	17.0	$1,2 \times 10^4$	0.0001

[a]from SAS type 1 (sequential) F-test for effect.
Conventions as in Table 7. Categorical effects in bold. Covariance parameter estimate for random effect survey 0.19 (CL 0.10–0.49).

Table 11. Anagach bog model A3 parameter estimates.

Parameter	Estimate	SE	DF	P(t)
Intercept	−6.976	1.135	585	0.0001
Kernel	2.637	0.315	1166	0.0001
Entrance	0.00873	0.00385	819	0.024
Entrance^2	−0.00792	0.00432	817	0.067
Entrance^3	0.00250	0.00151	815	0.097
Track	0.00742	0.00289	814	0.010
Track^2	−0.01865	0.006415	813	0.0037
Be + Bc	0.009781	0.002876	821	0.0007
(Bc)^2	$−2.766 \times 10^{-8}$	0.9841×10^{-8}	818	0.0051

Conventions as in Table 7. Covariance parameter estimate for random effect survey: 0.30 (CL 0.10–3.13).
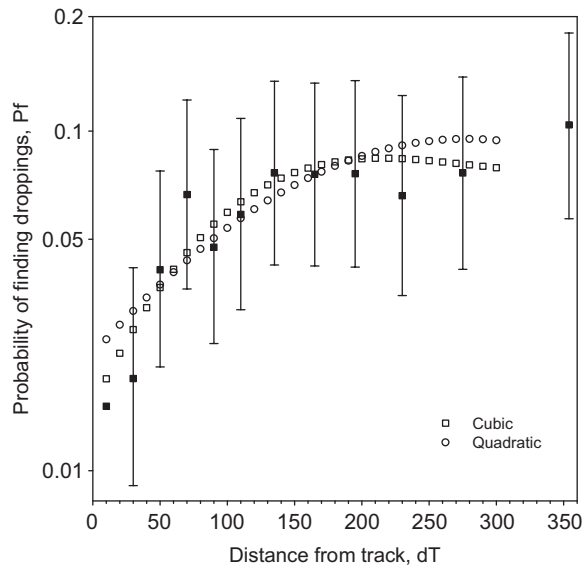
Figure 11. Quadratic and cubic probability trajectories for dT compared with band-based (■, bars 95% CL) model, Glenmore. Note the better agreement of cubic with band-based near the y-axis.

two exceptions. At Glenmore, well-built gravelled roads heavily used by forestry vehicles and people (expert rank 2) went along with lower estimates of Pf than footpaths used heavily by people but little or not at all by vehicles (expert rank 3). With hindsight, this was probably because people and dogs caused more disturbance than vehicles. At Anagach, expert ranks 2 and 3 were reversed by the Pf estimates. This was inconsequential because both were included in the less-used class.