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ORIGINAL PAPER

Responses of red deer (*Cervus elaphus*) to regular disturbance by hill walkers

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Abstract Disturbance to wildlife from human recreational activities is increasing as remote areas become accessible to greater numbers of people. We used Global Positioning System tracking collars to monitor the movements of red deer (*Cervus elaphus*) stags (n=8) in a herd whose feeding grounds lie close to a popular walking track in the Highlands of Scotland. The track is used by around 20,000 walkers per year and is busiest in summer and at weekends. In a 2-year study, the locations of collared deer were recorded at 2-h intervals on typically busy days (Sundays: mean number of walkers=204) and quiet days (Wednesdays: mean number of walkers=49) during May and June. The deer were consistently further from the track on Sundays than Wednesdays (371 vs 286 m) and moved greater distances between fixes (365 vs 308 m). The amount of time spent (percentage of total fixes) in the small area of grassland closest to the track was lower on Sundays than Wednesdays (6% vs 13%). Although 97% of walkers use the track during the day (between 0800 and 2000 h), there was no evidence of compensatory use of grassland at night, when the deer moved to higher ground dominated by heather moorland. The results demonstrate that animals which appear to be habituated to regular disturbance within their home territory may nevertheless alter their behaviour and potentially diet composition, as a result of that disturbance.

Keywords Behaviour · Disturbance · Global positioning system (GPS) · Habitat · Red deer · Movement

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Introduction

Disturbance to wildlife from human recreational activities has become an increasing matter for concern, as greater leisure time and improved transport systems have allowed more people access to hitherto undisturbed areas (Staines and Scott 1994). This brings with it the possibility of effects on the welfare and/or productivity of wildlife, in cases where disturbance alters behaviour patterns. Reduced calving rates in elk *Cervus elaphus canadensis* have been linked to human disturbance (Philips and Alldredge 2000), as have increased heart rates in sheep (MacArthur et al. 1979, 1982) and birds (Weimerskirch et al. 2002; Ackerman et al. 2004; Ellenberg et al. 2006) and increases in energy expenditure in a range of species (Speakman et al. 1991; Staines and Scott 1994; Regel and Putz 1997; Stock and Hofeditz 1997; Wolfe et al. 2000). Disturbance has also been shown to alter habitat use by wild ungulates (Gander and Ingold 1997; Jiang et al. 2009; Jayakody 2005), with the potential for altering diet composition if the source of disturbance coincides with a particular habitat type.

It is well-recognised that the effect of disturbance can vary with its predictability; unexpected events, such as hill walkers occasionally wandering 'off-track', are known to have greater effects on behaviour than expected events, such as walkers appearing regularly on established paths

(Shultz and Bailey 1978; MacArthur et al. 1982; Cassirer et al. 1992; Staines and Scott 1994; Tidhar 2000). However, animals which appear to be habituated to regular disturbance within their home territory could still be altering their behaviour in some way, and it has been argued that even quite small reductions in food quality or intake can have implications for productivity and survival in the long-term through a multiplier effect (White 1983).

A number of studies of disturbance to wildlife have observed the direct consequences of encounters with people or machines, for example with mule deer, *Odocoileus hemionus* (Freddy et al. 1986; Miller et al. 2001; Stankowich and Coss 2006), reindeer, *Rangifer tarandus* (Reimers et al. 2006), fallow deer, *Dama dama* (Langbein and Putman 1992), bison, *Bison bison* (Fortin and Andruskiw 2003), elk, *C. elaphus canadensis* (Borokowski et al. 2006), sika deer, *Cervus nippon* (Borokowski 2001) and brown bears, *Ursus arctos* (Rode et al. 2006). Other studies have compared the distribution patterns of animals with those of humans in areas used for recreation (Nellemann et al. 2000; Jayakody 2005; Manor and Saltz 2005; Galanti et al. 2006; George and Crooks 2006). In this study, our approach was to look at the direct consequences of recreational disturbance by tracking animals with GPS (Global Positioning System) collars. GPS collars allow intensive and relatively accurate positional monitoring, which is necessary for quantifying disturbance effects, without the extra cost and risk of further disturbance that would be incurred if the same data were to be collected with field observation methods.

Our study animals were a herd of male red deer (*Cervus elaphus*) in a mountainous region of Scotland which is popular with hill walkers and mountaineers. The deer traditionally live and feed close to one of the main access routes into the mountains for a large part of the year and are thus exposed to regular disturbance. In order to test for disturbance effects, we monitored the locations of collared individuals while they were resident within 2 km or so of the track; comparing days with typically high and typically low numbers of walkers. Some preliminary results of this study were reported earlier (Sibbald et al. 2001).

Methods

Study area

The study area was the Mar Lodge Estate in the Grampian region of Scotland. The Estate covers 29,340 ha and lies on the southern edge of the Cairngorm mountain range, ranging in altitude from 300 to 1,309 m. Vegetation at low to intermediate elevations (300 to 800 m) in this area comprises a mosaic of wet and dry heathland communities dominated by ericaceous species (*Calluna vulgaris* and *Erica* spp.), blanket bog and *Molinia*-dominated rough grasslands. The valley bottoms also contain areas of native Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) forest and some smooth grasslands (*Agrostis and Festuca* spp.). Mar Lodge Estate is owned by the National Trust for Scotland, an organisation which encourages public access for recreational purposes. Well-established tracks run through the estate, providing access to some of the most popular walking routes in the Cairngorm mountains. At the time of the study (1998–1999), there were estimated to be over 4,000 red deer (*C. elaphus*) ranging within the estate (personal communication Alistair Clunas, National Trust for Scotland).

The study site was Glen Lui (57° N 3°35′ W), which features a shallow river with some relatively good-quality smooth grassland either side of it and a rough walking track running along the valley bottom (Figs. 1a and b). There are areas of rough grassland close to the track and some areas of woodland. The surrounding hillsides are dominated by heather moorland with some grass/heather mosaics interspersed. The numbers of walkers using the Glen Lui track are routinely recorded by means of an automatic counter beside Derry Lodge (Fig. 1), which records the number of times that an infra-red beam is interrupted every hour. Estate records show that around 20,000 walkers use the track each year, with peak daily counts during the summer months (May to August) and significantly higher counts at weekends than during the week (Gardiner, 2000), and the data collected during the study were consistent with those records (Figs. 2 and 3). Deer hunting in the area is strictly controlled and only carried out by authorised personnel between the beginning of July and the middle of February.

Animals

The study animals were eight mature male red deer (stags), selected from a herd of over 200 animals who traditionally live and feed in Glen Lui from early November until the beginning of July, when they disperse and move away onto higher ground until the end of the rut (mating season; S. Cumming, personal communication). We fitted GPS collars to four stags at the end of March in 1998 and to another four stags at the end of March in 1999, and removed the collars after approximately 11 months in each case. In order to fit and remove the collars, a wildlife veterinarian, who was also an expert marksman, shot the stags with tranquiliser darts (Immobilon, Vericore, UK) from a vehicle at a range of about 30 m, while the stags were close to one of the feeding sites. Each year we selected animals for collaring on the basis that they came within range of the dart gun, were large enough to carry the collars and were in good health. The deer were sedated for 10–15 min only, while the collars were fitted, and rejoined the herd immediately afterwards. We did not observe any adverse

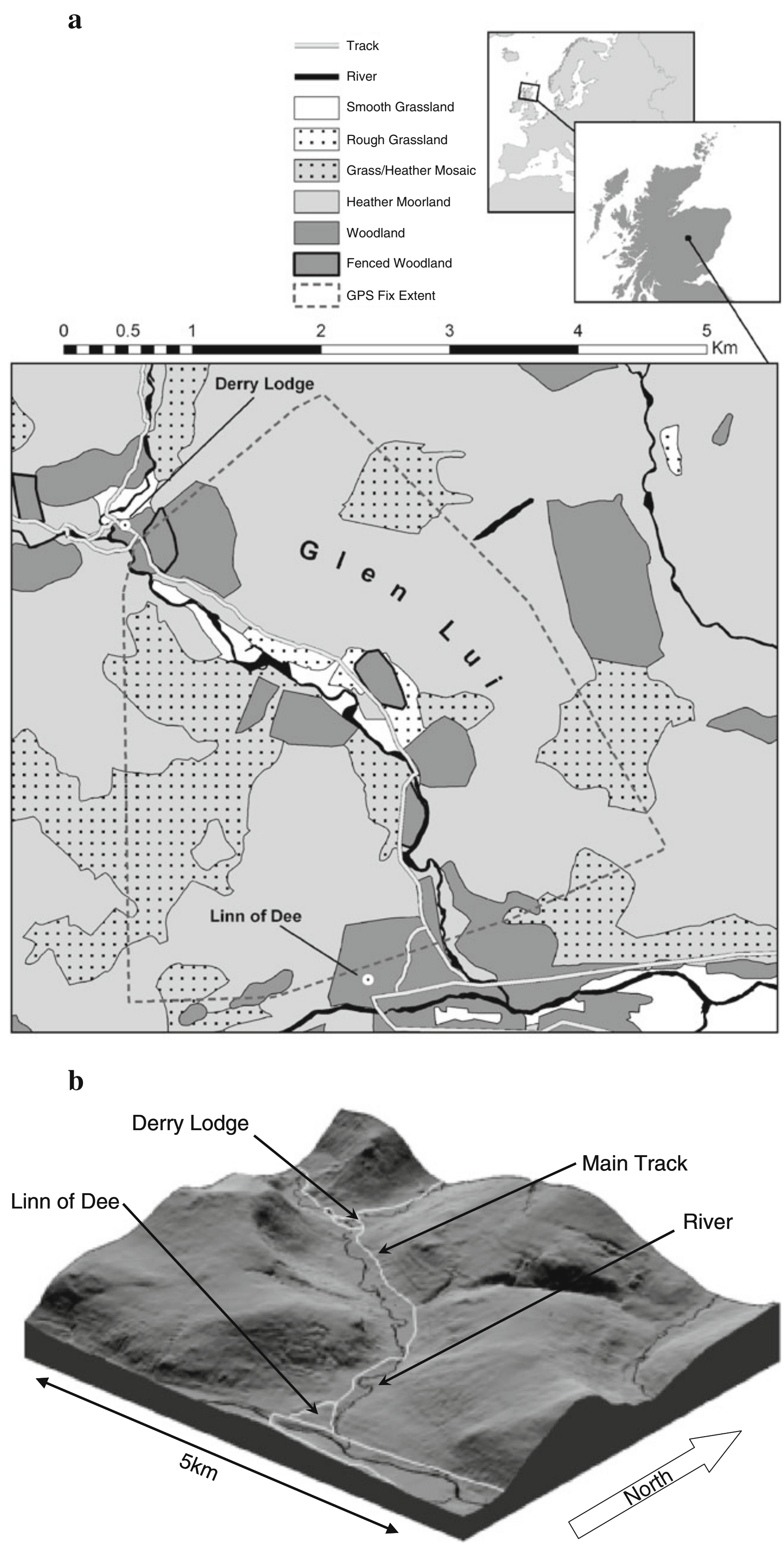

Fig. 1 **a** Map of Glen Lui showing the walking track from *Linn of Dee* to *Derry Lodge*, the main habitat types identified in the surrounding area and the GPS Fix Extent (the Minimum Convex Polygon containing the GPS fixes), and **b** 3-D topographical representation of the same area, showing the valley with the *main track* and *river* running through it and the surrounding hills

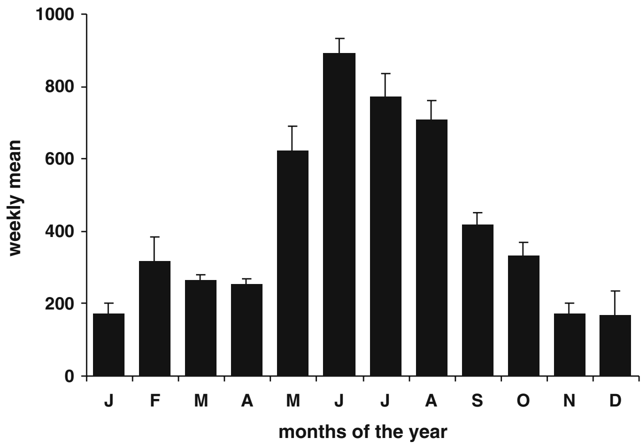

Fig. 2 Mean number of walkers counted on the Glen Lui track each week, for the different months of the year, with *SE bars*

effects on behaviour as a result of either this procedure or of wearing the collars. Experienced deer managers examined the teeth and estimated all the collared animals to be between 5 and 12 years of age when the collars were fitted.

Operation of GPS collars

We used six-channel GPS 1000 wildlife tracking collars, software version 2.11 (Lotek Engineering Inc., Newmarket, Ontario, Canada), with differential correction and remote download facilities. The collars were powered by high-density lithium batteries and were able to store data for up to 1,680 fixes. We created the fix schedules in advance using GPSHost 1000 software, version 3.08 (Lotek Engineering Inc.), and programmed the collars to take fixes at 4-h intervals in 1998 and 2-h intervals in 1999. Fixes were also taken at 2-h intervals on Sundays and Wednesdays in 1998. We downloaded data from the collars remotely onto a portable computer, via a UHF modem, using a GPS Animal Location System Command Module (Lotek Engineering Inc., Newmarket, Ontario, Canada). We carried out the downloading process when the collars were within 1–2 km of the command module.

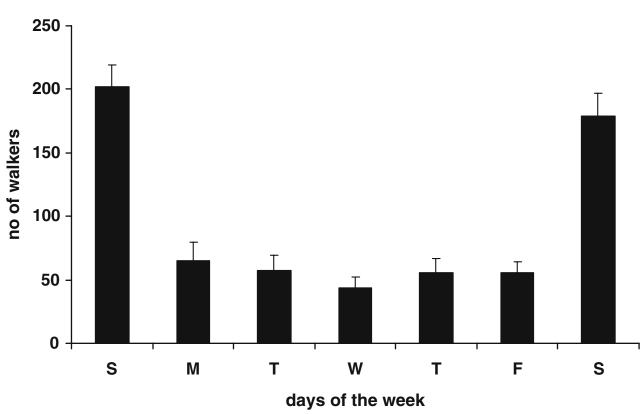

Fig. 3 Mean number of walkers on the Glen Lui track each day of the week during the study period, with *SE bars*

Processing of GPS data

We differentially corrected the fixes using N4 Post-processing software (Lotek Wireless Inc., Canada), together with data from a 12-channel GPS Pathfinder base station equipped with Path Finder Community Base Station (PFCBS) software, version 2.67 (Trimble Navigation Ltd., Sunnyvale, California, USA). The base station was situated 86 km east of the study site. In previous work with the same type of GPS collars, Adrados et al. (2003) showed that >90% of 3D fixes with a Dilution of Precision (DOP) of <10 were within a 10-m error radius. Consistent with this and other studies (Moen et al. 1996, Rempel and Rodgers 1997), we discarded all data with a DOP of >10. We then converted the fix data, expressed as latitude and longitude, to Ordnance Survey Great Britain National Grid (OSGB36) coordinates and imported them into ArcView 3.2 (Environmental Systems Research Institute, California, USA). As an indication of collar accuracy, we scheduled a collar to take a fix every 4 h and left it stationary, about 5 km from the study area, for a period of 2 weeks. The data showed 88% of fixes to be within 10 m and 63% within 5 m of the mean fix location.

Assessment of disturbance effects

For our disturbance study we used the 2-h fix data collected during a 7-week period in 1998 (year 1) and an 8-week period in 1999 (year 2), starting on the first Sunday in May in each case. This is a time of year when walker numbers are normally high (Fig. 2), but before the deer begin to disperse. We compared the mean distances of GPS fixes from the track and the mean distances between consecutive fixes on days that are normally busy (Sundays) and days that are normally quiet (Wednesdays; Fig. 3) over the 15 weeks. We chose not to base our analysis on the actual numbers of walkers recorded each day, since we had no information about the idiosyncrasies of individual walkers or groups of walkers, whether they moved off the track or whether they were accompanied by dogs. Nor could we tell how far the collared deer were from the track or from other herd members when the walkers appeared, since counts were only summarised every hour. For these reasons, as well as the occasional failure of the counter, we decided to compare mean values for typically busy and typically quiet days. However, as there are no clues available to the deer in Glen Lui to indicate which day of the week it is, other than the varying number of walkers on the track, any systematic differences in behaviour between Sundays and Wednesdays are most likely to have been due to disturbance from the walkers. Since around 97% of walkers on the Glen Lui track were counted between 0800 and 2000 hours (Fig. 4), we calculated separate means for the 'day' period (fixes taken 2 h from 1000 to 2000 hours inclusive) and the 'night' period (fixes taken 2 h from 2200 to 0800 hours inclusive), as there would have been virtually no disturbance from walkers at night. During May and June, sunrise and sunset range between 0521 and 0417 hours and 2052 and 2207 hours, respectively, so that 'night' did not coincide exclusively with the hours of darkness.

We classified fixes according to habitat type, using a GIS-based vegetation map of the area derived from The Land Cover of Scotland 1988 (LCS88) database (MLURI 1993). For the purpose of this study, we grouped the LCS88 habitat categories into five main habitat types, namely, rough grassland (*Nardus* and *Molinia* spp), smooth grassland (*Agrostis* and *Festuca* spp), woodland (both coniferous and broadleaved spp), heather moorland (dwarf shrub, *Calluna* spp) and mosaics of rough grassland and heather moorland, as illustrated in Figs. 1a and b. The minimum convex polygon of the GPS fixes (Fig. 1a) was created using the Hawth's Tools (Beyer 2004), *Create Minimum Convex Polygons* tool. The mean distance of each of the habitat types from the track was estimated by creating a fine scale (1-m grid) raster map of the distance to the track, using the ArcMap 9.3 (ESRI 2009), *Straight Line Distance* tool, and then using the Hawth's Tools (Beyer 2004), *Zonal Statistics* tool, to calculate the mean value of this distance raster for each habitat type within the minimum convex polygon of the fixes. We estimated the mean altitude of each fix location using a 10-m grid digital elevation model (Ordnance Survey Landform Profile).

Statistical analysis

All statistical analyses were carried out by analysis of variance using the ANOVA command in Genstat (Lawes Agricultural 2003), declaring day type (Sunday or Wednesday) and period (day or night) as treatment factors. Day number and year were declared as blocks, since different individuals were collared each year and since the day and night periods within any 24-h period cannot be considered to be independent. We compared mean distances from the track and mean distances between consecutive fixes, both across all habitat types and within each habitat type. We also compared the mean percentage of fixes in each habitat type. For each day, we used the day and night mean values for the group of collared deer, rather than using individual animal data, since we do not know whether the collared deer were acting independently or moving with the herd. Replication was achieved by carrying out the measurements in two different years and by making measurements on a total of 15 Sundays and 15 Wednesdays over those 2 years. We treated days as independent, since it is unlikely that there could be any carry-over effects of disturbance from one measurement week to the next. Since Sundays always follow Wednesdays and vice versa, it is also likely that any carry-over effects of disturbance would have reduced rather than enhanced the differences between day types. There was no replication at the level of the herd. When analysing percentages, we used angular transformed proportions to equalise variances and normalise the data. In these cases, the results are expressed as mean percentages, but the F and P values quoted are those derived from the analyses of angular transformed proportions.

Results

Number of walkers on the track

Due to technical problems with the counter, hill walker data for 4 weeks in year 1 and 1 week in year 2 of the 15-week

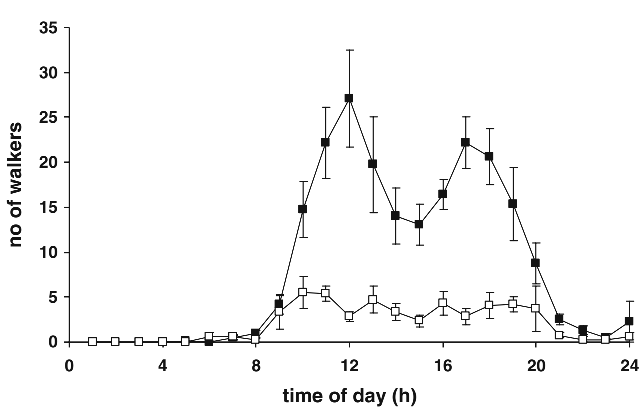

Fig. 4 Mean number of walkers recorded each hour of the day (counted during the preceding hour) on Sundays (*black square*) and Wednesdays (*white square*) during the study period, with *SE bars*

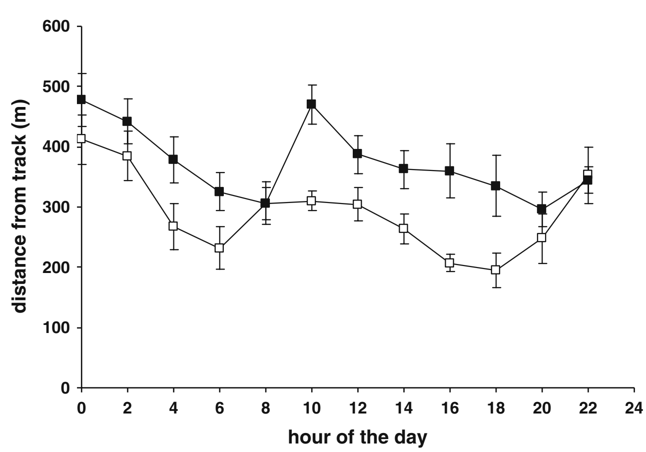

Fig. 5 Mean distance of deer GPS fixes from the track every 2 h on Sundays (*black square*) and Wednesdays (*white square*), with *SE bars*

Table 1 Mean distance of deer GPS fixes from the track (meters) during the day (0800–2000 hours) and night (2000–0800 hours) on Sundays and Wednesdays, classified by habitat type, with standard error of difference (SED) for day-type comparison; plus the mean distance of all possible locations within the minimum convex polygon of the GPS fixes (MCP)

	Day		Night			
Habitat type	Sunday	Wednesday	Sunday	Wednesday	SED	MCP
Rough grassland	118	107	112	88	13.1	106
Smooth grassland	191	182	185	177	7.1	173
Woodland	393	344	266	296	48.5	350
Heather moorland	433	325	443	390	55.2	843
Grass/heather mosaics	516	323	356	175	42.9	1,085

disturbance study were missing, but for the remaining weeks the counter showed four times as many walkers on Sundays than on Wednesdays (204.0 vs 49.4, $F_{1,14}$=111.28, P<0.001), with 97% (±1.0%) passing between 0800 and 2000 hours each day (Fig. 4).

Distance of deer from the track

Across all habitat types, the mean distance of deer fixes from the track was greater on Sundays than Wednesdays (371 vs 286 m, $F_{1,27}$=4.92, P=0.035). The day-type effect appeared to be stronger during the day, with the peak day-time distance at 1000 hours (Fig. 5) coinciding with a rapid rise in the number of walkers (Fig. 4). However, there was no significant effect of period on distance from the track ($F_{1,28}$=0.78, P=0.384) or any interaction between day-type and period effects ($F_{1,28}$=1.38, P=0.249). Within the grass/heather mosaic vegetation, fixes were further from the track on Sundays than Wednesdays ($F_{1,24}$=18.95, P<0.001, Table 1) and further away during the day than at night (420 vs 266 m, $F_{1,16}$=23.53, P<0.001). There were no significant effects of day type or period on mean distances from the track within the other habitat types (Table 1).

Percentage of fixes in different habitats

There were fewer fixes in rough grassland on Sundays than Wednesdays (5.5% vs 12.6%, $F_{1,27}$=14.75, P<0.001), but effects of day type in the other habitats were not significant (Table 2). There was an effect of period on the distribution of fixes across habitats, with more fixes during the day than the night in smooth grassland (24.3% vs 14.3%, $F_{1,28}$=4.86, P=0.036) and the grass heather mosaics (21.1% vs 10.2%, $F_{1,28}$=10.89, P=0.003) and more fixes at night than during the day in heather moorland (60.2% vs 36.6%, $F_{1,28}$=25.96, P<0.001; Table 2). At night, the deer tended to be at higher altitudes between 2200 and 0200 hours (Fig. 6), a period that coincides with the hours of darkness at that time of year. There were no significant interactions between day-type and period effects on the percentage of fixes in the different habitats.

Distance between fixes

The mean distance between consecutive 2-h fixes was significantly greater on Sundays than Wednesdays when analysed across all habitats (365 vs 308 m, $F_{1,27}$=4.66, P=0.040) and also tended to be greater on Sundays in the smooth grassland ($F_{1,24}$=3.71, P=0.066), with the effect most apparent during the day (Table 3). The mean distance between fixes was greater during the day than at night in heather moorland (412 vs 252 m, $F_{1,27}$=6.39, P=0.018), but there were no other effects of day type or period when the data were analysed within habitats (Table 3).

Discussion

The results of this study suggest that the deer moved away from the source of disturbance when the track was busy

Table 2 Mean percentage of deer GPS fixes within the five main habitat types in Glen Lui, during the day (0800–2000 hours) and night (2000–0800 hours) on Sundays and Wednesdays, with SED for day-type comparison

	Day		Night		
Habitat type	Sunday	Wednesday	Sunday	Wednesday	SED
Rough grassland	5.0	14.0	5.9	11.2	2.01
Smooth grassland	22.2	26.3	15.5	13.1	4.0
Woodland	9.9	6.9	7.9	5.5	3.18
Heather moorland	39.3	34.0	58.8	61.6	5.73
Grass/heather mosaics	23.6	18.9	11.9	8.6	5.08

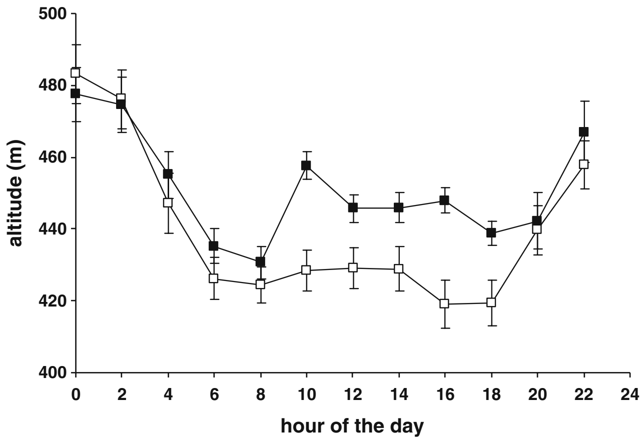

Fig. 6 Mean altitude of deer GPS fixes every 2 h on Sundays (*black square*) and Wednesdays (*white square*), with *SE bars*

with walkers. The disturbance effect tended to last over the full 24 h, even though the track was quiet at night, but the effect was noticeably stronger during the day. However, habitat type is confounded with distance from the track in Glen Lui, making the situation rather more complicated (see Table 1), as moving away is likely to involve a change of habitat, particularly when animals are close to the track. This was confirmed by the within-habitat analyses, which showed that a simple difference in distance between Sundays and Wednesdays was only apparent within the grass/heather mosaics, which extended much further from the track than the grassland. Since all the rough grassland lies within about 300 m of the track, moving as little as 100 m is more likely to take deer into another habitat type than further away within the grassland. This was borne out by the results, which showed less fixes in rough grassland on Sundays than Wednesdays. One might have expected that disturbance would also result in deer moving off the smooth grassland, but this effect was very small. However, smooth grass is known to be a preferred vegetation type for red deer (Gordon 1989) and it may be that the deer were more strongly motivated to stay on the smooth grass. Indeed, the tendency to move further between fixes on the smooth grassland suggests that although the deer were disturbed on Sundays, they tended to respond by moving more within the smooth grassland rather than moving away to a different habitat type. This is consistent with a previous finding that deer in disturbed grassland move more and show more vigilance behaviour than deer in heather or woodland habitats (Jayakody et al. 2008). More frequent fixes taken on a few selected days in July, after the deer had moved away onto the higher ground, also indicated that they moved further on Sundays than Wednesdays; sometimes as much as twice the distance (Sibbald et al. 2001). In that case, disturbance will have been from walkers who had left the Glen Lui track and were moving along the various smaller tracks on the higher ground. Disturbance did not appear to affect the deer in Glen Lui when they were in woodland, even though some of the woodland was quite close to the track, but this is not particularly surprising given the greater amount of cover provided by woodland vegetation compared to other habitat types.

Simple avoidance of areas associated with disturbance does not necessarily affect animal performance, even if disturbance occurs close to preferred feeding grounds. For example, a study of shore birds (black-tailed godwits *Limosa limosa*) found that in spite of their consistent flight responses when humans entered their feeding grounds, there were no effects on the number of individuals supported by the food supply (Gill et al. 2001). This could be the result of compensatory use of the preferred feeding grounds during periods without disturbance. However, we found no indication of any compensatory use of grassland in this study, as the percentage of fixes on all types of grassland was low at night on both Sundays and Wednesdays. This may have been because the deer tended to move to higher ground during the hours of darkness and the higher ground was dominated by heather moorland. This is consistent with previous observations that red deer in this kind of terrain move downhill in the mornings to feed on the valley bottoms and move back onto the lower slopes of the hills in the evenings (Clutton-Brock et al. 1982). There is evidence that sheep will also move to higher ground during the night (Bowns 1971), as will cattle (Sibbald et al., unpublished data). Compensation could have been achieved by changes in intake rate but, although the GPS data give an idea of the relative time spent in different habitat types by the deer, we have no information

Table 3 Mean distance between consecutive 2-h fixes during the day (0800–2000 hours) and night (2000–0800 hours) on Sundays and Wednesdays, classified by habitat type, with SED for day-type comparison

	Day		Night		
Habitat type	Sunday	Wednesday	Sunday	Wednesday	SED
Rough grassland	448	451	511	570	84.4
Smooth grassland	443	276	390	380	45.6
Woodland	410	359	200	408	95.5
Heather moorland	393	431	289	216	59.3
Grass/heather mosaics	440	339	397	465	99.0

about the amount of time spent feeding or the biomass available in the different areas.

As well as the potential for disturbance to affect performance through diet composition and intake, disturbance can also compromise the welfare of wildlife species through increased stress. Jayakody et al. (2008) found that deer exposed to a similar amount of disturbance increased their vigilance, a behaviour that can be associated with physiological stress (Monclus et al. 2005; Deiss et al. 2009). Symptoms of stress have been found in several species following human disturbance, for example penguins (Ellenberg et al. 2009), quail (Bertin et al. 2008), wolves and elk (Creel et al. 2002), although welfare is not necessarily affected (Creel et al. 2002; Martin and Reale 2008).

The fact that the herd selected for this study regularly over winter in Glen Lui, in spite of the relatively large numbers of walkers that come to the area in spring and summer, suggests that they are habituated to the presence of walkers. However, our results show systematic differences in the behaviour of the deer on typically busy and typically quiet days. Habituation to disturbance on frequently-used walking tracks has been documented in other wild animals, for example mule deer (Cornett et al. 1979) and grizzly bears (Jope 1985), but repeated presentation of a stimulus does not necessarily lead to extinction of the response (McSweeney and Swindell 2002) and it seems unlikely that the deer in Glen Lui will stop responding to the walkers, since the herd has been feeding there for many years. Although we were not able to determine whether the deer suffered any increase in stress or change of diet composition in this study, the results suggest that, even in a situation where animals appear to be habituated to human disturbance, long-term population effects due to small but persistent changes in behaviour cannot be ruled out.

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