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Habitat type determines the effects of disturbance on the breeding productivity of the Dartford Warbler *Sylvia undata*

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Numerous studies have examined the causes and impacts of human disturbance on birds, but little is known about how these impacts vary among habitats. This is of applied importance both for predicting bird responses to changes in disturbance and in planning how to reduce disturbance impacts. The Dartford Warbler *Sylvia undata*, a key heathland breeding species, occupies territories in a range of heathland types. Three territory habitat groups were identified: heather-dominated territories, heather territories with significant areas of European Gorse *Ulex europaeus* and territories containing Western Gorse *U. gallii*. Productivity was significantly affected by the timing of breeding in all habitats, but disturbance only appeared to have a significant impact on the productivity of birds in heather territories. Disturbance events in heather territories delayed breeding pairs for up to 6 weeks. This significantly decreased both the number of successful broods raised and the average number of chicks fledged per pair. Nests situated close to territory boundaries in heather territories, with high numbers of disturbance events, were more likely to fail outright. It was determined that an average of between 13 and 16 people passing through a heather territory each hour would delay breeding pairs sufficiently to prevent multiple broods.

Many studies have examined the possible causes and impacts of human disturbance on birds (see reviews by Hockin *et al.* 1992, Carney & Sydeman 1999), but little is known about how these effects vary between habitats. This potential variation is of applied importance, having implications for access planning and management both within and among sites. We studied the impact of disturbance on the Dartford Warbler *Sylvia undata*, which in the UK breeds almost exclusively on the lowland heaths of southern England (Bibby & Tubbs 1975, Gibbons & Wotton 1996) where it occupies territories in a variety of heathland habitat types.

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Lowland heaths are a highly fragmented, much diminished habitat (Moore 1962, Webb & Haskins 1980, Rose *et al.* 2000) and have been classified in the UK as a Biodiversity Action Plan priority habitat. The Dartford Warbler is a bird of conservation concern (Bibby 1978, Westerhoff & Tubbs 1991, Gibbons & Wotton 1996) and is among the most characteristic inhabitants of the heaths of southern England. Past studies have shown that Dartford Warblers are critically dependent on this declining habitat (Bibby & Tubbs 1975, Robins & Bibby 1985, Westerhoff & Tubbs 1991). Heaths are found in densely populated parts of the UK and are used extensively for outdoor recreation. Thus, there is scope for significant impacts of disturbance on the wildlife of heathlands.

Lowland heathland is dominated by heather or ling *Calluna vulgaris* but characteristically supports

gorse species such as European Gorse *Ulex europaeus*, Western Gorse *U. gallii* and Dwarf Gorse *U. minor*. The breeding biology and feeding ecology of the Dartford Warbler on UK heathlands have been studied by Bibby (1979a, 1979b). Catchpole and Phillips (1992) found that Dartford Warblers have a strong positive relationship with *U. europaeus*, and territories containing more *U. europaeus* produced more young. Gorse provides a rich source of invertebrate prey, protection from predators and shelter in poor weather (Catchpole & Phillips 1992, van den Berg *et al*. 2001). *U. minor* currently plays little role in Dartford Warbler ecology. However, with increasing numbers in Dorset, Dartford Warblers are colonizing more heaths dominated by *U. gallii* (Anon. 1994–2004). This gorse species occurs most commonly on heaths located near the urban centres of Bournemouth and Poole in Dorset (Bullock *et al*. 2000).

There has been a new focus on disturbance issues since the introduction of the Countryside and Rights of Way (CRoW) Act in 2000 (Bathe 2007). This Act created a statutory right of access off designated rights of way on foot for open-air recreation to mountains, moors, heathlands, downs and registered common land and encourages the provision of additional footpaths (Bathe 2001, 2007). However, the Act allows mitigation measures, such as closure of access land, diversion of footpaths and keeping dogs on short leads from March to July, to help protect breeding wildlife.

Animals often respond to human disturbance as they would to potential predators (Frid & Dill 2002, Finney *et al*. 2005). The responses are well documented for a range of species (see reviews by Hockin *et al*. 1992, Hill *et al*. 1997) and include elevated heart rate (Weimerskirch *et al*. 2002), increased defensive behaviours (Anderson *et al*. 1996, Reby *et al*. 1999) and the avoidance of high-risk areas, either completely or by using them for limited periods only (Gill *et al*. 1996, Liley 1999, Finney *et al*. 2005, Liley & Sutherland 2007). Birds may also be affected more directly, through egg or chick mortality caused by trampling or greater exposure to poor weather or predators (Liley & Sutherland 2007). Consequently, where levels of human disturbance are high, human activities can reduce reproductive success and individual survival (Hockin *et al*. 1992, Goodrich & Berger 1994, Burger *et al*. 1995) and population size (Liley & Sutherland 2007). Our interest is in establishing the precise impacts of recreational disturbance on the Dartford Warbler, if any, and determining the most appropriate management techniques required to minimize these impacts.

METHODS

Study area

Nineteen heathland sites, situated in both rural and urban areas of Dorset (Fig. 1), and covering a range of lowland heath habitat types, were chosen for study: 12 during 2003 and an additional seven in 2004 (Table 1).

Territories

Territory mapping followed the procedure established by Bibby *et al*. (2000). Territory boundaries were mapped around the registrations of all birds observed during surveys on scaled site maps, and by recording the GPS coordinates of their positions, which were then transferred to aerial photographs on MapInfo (Version 4.12). Records of male territorial displays and regular singing posts helped to identify territory boundaries. Territories were visited weekly from April to August, and bi-weekly throughout the winter. Any seasonal changes in their size and extent were recorded. Territory perimeters and total areas were calculated using MapInfo.

Reproductive success

Dartford Warblers may produce up to three broods in a single year and enjoy relatively high nesting success (Bibby 1977). Their nests are placed in dense vegetation and are equally difficult to locate in all habitat types. Although breeding activity in each territory was continually monitored, relatively few nests with eggs were found during incubation and it was only in 2004 that an accurate measure of starting times (day 1 of incubation of first clutches) could be assessed. Nest start dates were numbered (1 = January 1). Frequency of nest visits depended on the stage at which the nest was found. If nests were found during incubation, so that the lay date (the date of laying the first egg) was not known, then nests were visited every 2 days; otherwise nests were visited every 3 days. Chicks were ringed 6–8 days from hatching (Cramp 1992), with a unique combination of colour rings and a British Trust for Ornithology metal ring. Nest monitoring continued until the chicks fledged or died.

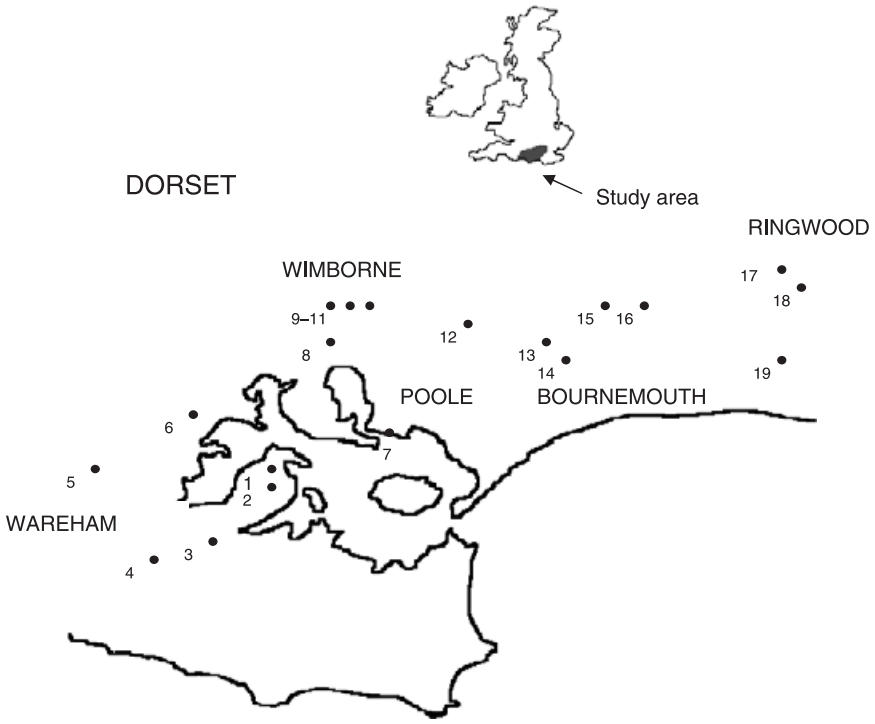

Figure 1. Map of Dorset showing the approximate locations of the 19 study sites.

Table 1. The heathland sites studied between 2003 and 2004, including site disturbance levels and the average number of territories of each habitat type at each site.

Site name		Site size (ha)	Observed area (ha)	Average no. of territories (2003–05)			Disturbance level*
				Heather	*U. europaeus*	*U. gallii*	
1	Arne – Grip	30.5	30.5	0	10	0	1
2	Arne – Coombe	35.9	35.9	1	13	0	1
3	Stoborough	110.0	30.4	0	4	0	1
4	Grange	39.8	39.8	0	7	3	1
5	Great Ovens†	42.5	42.5	0	2	11	3
6	Holton	46.1	46.1	0	12	0	1
7	Ham Common	24.8	21.4	0	0	3	4
8	Upton	223.1	26.5	0	0	11	3
9	Corfe Hills 1†	8.5	8.5	0	0	2	1
10	Corfe Hills 2†	18.2	15.1	0	0	5	1
11	Corfe Hills 3†	7.3	7.3	0	0	3	1
12	Canford†	407.2	40.4	0	0	5	3
13	Bourne Valley	6.3	6.3	0	0	3	4
14	Talbot	22.3	22.3	0	0	10	3
15	West Parley	123.2	21.9	6	10	0	2
16	Ferndown†	51.5	51.5	0	0	10	3
17	Avon CP North	113.0	113.0	13	5	0	2
18	Avon CP South	62.7	62.7	2	8	0	2
19	Town Common†	227.5	20.4	5	1	0	1

*1: 0.0–7.0, 2: 7.1–14.0, 3: 14.1–21.0, 4: > 21.0 (disturbance events per hour).
†2004 only.

Table 2. Variables measured during 2004 habitat surveys.

Vegetation composition (% cover)	Vegetation height (cm) (% cover at:)
Lichen	Height 1: 0–20 cm
Moss	Height 2: 21–40 cm
Grass	Height 3: 41–60 cm
Common Heather (*Calluna vulgaris*)	Height 4: > 60 cm
Bell Heather (*Erica cinerea*)	Min. (minimum vegetation height)
Cross-leaved Heather (*Erica tetralix*)	Max. (maximum vegetation height)
European Gorse (*Ulex europaeus*)	
Western Gorse (*Ulex gallii*)	
Dwarf Gorse (*Ulex minor*)	
Herbaceous species	
Trees (Pine *Pinus sylvestris*, birch *Betula pendula*/*B. pubescens*)	
Bare ground	
Debris	

Territory habitat variables

Habitat surveys were undertaken on ten heathland sites, spanning the full range of heathland habitat types, in order to describe and assess the dominant vegetation types used by Dartford Warblers. The variables measured are given in Table 2. Percentage cover variables were measured in replicated quadrats measuring 3×3 m, at intervals of 25 m, sampled along a diagonal transect across the longest axis of each territory. Consequently, the number of replicates per territory varied (mean ± sd) according to territory size, ranging from 5 to 50 (22.0 ± 8.4). The number of territories covered per site varied between 1 and 10 (4.0 ± 1.8).

Owing to the high degree of correlation between habitat variables, unrotated Principal Components Analyses (PCA) were performed on the correlation matrices to give a small number of mutually independent composite variables that summarized territory vegetation structure and composition (Field 2000).

Recreational disturbance

Sixteen sites were open to the public or allowed some access. Recreational activity was monitored on all sites in 2003 and 2004, and measured at two levels: at the site level along transect routes, and within sites at the territory level, at focal points within each territory. The number of human disturbance events, defined as any human activity that may have affected Dartford Warbler behaviour, was recorded while walking 1-h transects around these sites, and at focal watches. Every recreational user was noted and their activity recorded. Counts of disturbance events at territory centres gave an accurate assessment of the number of people per hour passing through each territory. In 2003, daily counts were repeated every month to assess changes in recreational disturbance over the breeding season. As the level of disturbance was not found to vary through the summer, a 12-h day (07:00–19:00 h) recreational disturbance profile was completed once for each site in 2004, based on transects carried out weekly on each site from March to August.

Measures of indirect disturbance, including the distance from the centre of the territory and the nest-site to the nearest path, road, building, car park (both official, a car park created for the site; and unofficial, a formal access point where there was room for cars to be parked) and the nearest authorized access point, were calculated using MapInfo. The degree of urbanization of a site was calculated using the percentage of urban cover within a 500-m band surrounding the site. All results are presented as means ± se unless otherwise stated. The logistic regression graph relating nest outcome to territory disturbance levels is presented according to the method devised by Smart *et al.* (2004).

RESULTS

Territory numbers

Ninety-eight and 106 territories were identified and monitored for disturbance during 2003 and 2004, respectively. In 2004, a total of 71 breeding pairs and 117 nests were observed throughout the year.

Table 3. Habitat variables, derived from the Principal Components Analysis. The percentage of variance explained by each PC is shown in parentheses. Correlation coefficients significant at < 0.001 are shown for each original variable with the PC. All variables describe the percentage cover of vegetation types/height classes, except for Min./Max. – the minimum and maximum height of vegetation, respectively.

PC1 (41.6%)		PC2 (19.6%)		PC3 (14.8%)	
Variable	Coefficient	Variable	Coefficient	Variable	Coefficient
C. vulgaris	−0.618	*U. gallii*	−0.590	*U. gallii*	−0.652
Height 2	−0.631	Height 3	−0.698	Height 1	−0.419
Bare ground	−0.461				
U. europaeus	0.678	*U. europaeus*	0.487	*C. vulgaris*	0.494
Height 4	0.894	Height 1	0.565	*C. cinerea*	0.401
Max.	0.803	Height 2	0.451	Height 3	0.472
Min.	0.807				

Territory habitat

The results of the PCA of territory habitat characteristics are given in Table 3. PC1 explained approximately 42% of the total variance in vegetation variables, with PC2 and PC3 together adding a further 34.4%. PC4 added less than 10% and is not described here. PC1 described a habitat gradient extending from areas of mature heather, with patches of bare ground (negatively correlated with PC1) to areas of tall *U. europaeus* (positively correlated with PC1). PC2 described an environmental gradient extending from areas of tall *U. gallii* (negatively correlated with PC2) to small, short patches of *U. europaeus* (positively correlated with PC2). Lastly, PC3 showed a habitat gradient ranging from low *U. gallii* (negatively correlated with PC3) to tall, mature heather (positively correlated with PC3).

Where *U. gallii* occurred on a heathland site, it tended to dominate, to the extent that areas of *U. gallii* and mature heather were not recorded in the same Dartford Warbler territory. The PC scores describe the characteristic territory habitat groups identified in this study:

(1) heather-dominated territories – those with *C. vulgaris* cover averaging 77.0% of the territory (1.35 ± 0.081 ha), described by positive PC3;

(2) *U. gallii* territories – those with *U. gallii* cover averaging 62.6% of the territory (0.709 ± 0.072 ha), described by PC2; and

(3) *U. europaeus* territories – those with significant *U. europaeus* cover averaging 17.1% (0.300 ± 0.033 ha), described by PC1.

As a result of these analyses of territory habitat variables, three types of territory habitat groups have been recognized in further analyses: heather-dominated territories, heather territories with significant *U. europaeus* and territories containing *U. gallii*.

Territory disturbance

Disturbance in Dartford Warbler territories ranged from no events to one every 1.33 min during the observation period. Overall, the number of disturbance events did not vary significantly between months over the breeding season (Kruskal–Wallis test: $H_{10} = 4.11$), although territories on heathland sites closely associated with recreation areas (e.g. picnic sites) did show a heightened disturbance peak during July and August. Eight types of human disturbance events were recorded (Table 4). Dog-walkers accounted for 72 and 60% of all disturbance events in 2003 and 2004, respectively. Disturbance data from 2003 and 2004 were pooled for the 12 sites sampled in both years, as there was no difference between them (*t*-test: $t = 1.77$, $P = 0.21$). There was a high correlation between the different types of disturbance measured, for example the number of people and the number of dogs (Spearman's rank coefficient test: $r_s = 0.88$, $P < 0.001$).

Timing of breeding and the influence of disturbance events

Breeding pairs exhibited a wide range of nest start times. Average start dates are given ± sd. In 2004, first broods began as early as 17 April and as late as 2 June The mean start date was 121.98 (1 May) ± 10.66 days. This difference between the first and last start dates

Table 4. The relative importance of different forms of recreational disturbance in Dartford Warbler territories, measured as the proportion of disturbance events recorded.

	No. (%) of observed disturbance events per 12-h day	
Cause of disturbance	2003 (n = 1644)	2004 (n = 1699)
Dog-walkers	1187 (72.2)	1014 (59.7)
Birdwatchers & naturalists	178 (10.8)	275 (16.2)
Walkers & joggers	139 (8.5)	201 (11.8)
Cyclists	59 (3.6)	95 (5.6)
Horse riders	47 (2.8)	27 (1.6)
Vehicles (cars, motorcyclists, tractors)	34 (2.1)	87 (5.1)

Table 5. Comparison of the reproductive output of breeding pairs in territories of different habitat types in relation to the timing of first broods using Spearman's Rank Coefficient Test. Late breeding pairs raised fewer broods, fewer successful broods and fledged fewer young in all habitat groups.

Breeding productivity	Territory habitat groups	r_s	n	Significance
No. of broods	Heather	–0.601	18	P = 0.004
	U. europaeus	–0.353	25	P = 0.042
	U. gallii	–0.511	25	P = 0.005
No. of successful broods	Heather	–0.795	18	P < 0.001
	U. europaeus	–0.382	21	P = 0.044
	U. gallii	–0.569	18	P = 0.007
No. of fledged chicks	Heather	–0.621	18	P = 0.003
	U. europaeus	–0.546	22	P = 0.004
	U. gallii	–0.655	18	P = 0.002

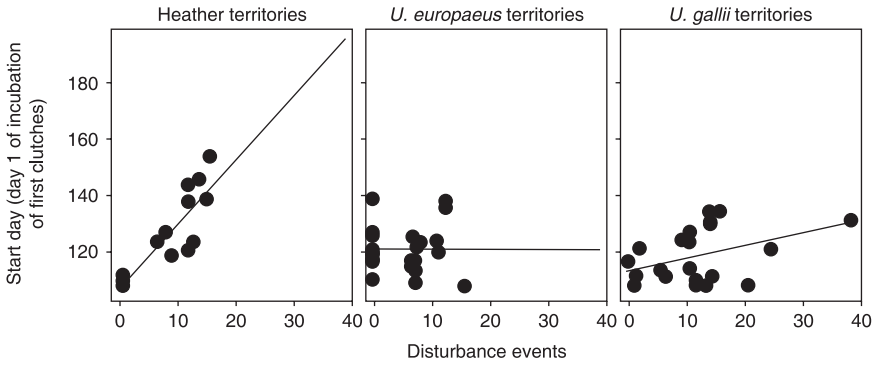

Figure 2. Correlations showing the relationships between the timing of first clutches and the number of disturbance events per hour in different territory types. Disturbance delayed the start of first broods significantly in heather-dominated territories.

of first broods was largest in heather-dominated territories at 46 days. The mean heather territory start date was 8 May (128.15 ± 14.78 days) compared with 1 May (121.56 ± 8.09 days) in *U. europaeus* and 27 April (118.96 ± 9.34 days) in *U. gallii*. Pairs that reared late first broods fared significantly worse overall than those with early first broods. Late first broods led both to fewer broods and fewer successful broods, overall, and to significantly fewer chicks being fledged per pair (Table 5). Although these trends were apparent in all territory habitat groups, they were more pronounced in heather and *U. gallii* territories.

Disturbance events clearly affected the timing of breeding. There was a significant negative relationship between the timing of first broods and disturbance rates on territories dominated by heather (Fig. 2:

Table 6. Non-parametric tests comparing breeding productivity of territories of different habitat types exposed to low vs. high levels of disturbance (Mann–Whitney *U*-tests, *Z* statistic, two-tailed test). Disturbance was measured as the average number of disturbance events per hour occurring at each territory. Low disturbance, < 10 events/h; high disturbance, > 10 events/h. Nests exposed to high levels of disturbance in heather territories raised fewer successful broods and fledged fewer young.

Territory habitat group	Low disturbance	High disturbance	*Z*	Significance
No. of broods				
Heather	1.42	1.50	–0.046	0.964
U. europaeus	1.62	1.80	–0.608	0.544
U. gallii	2.38	1.83	–1.703	0.088
No. of successful broods				
Heather	1.70	1.11	–2.481	0.012
U. europaeus	1.35	1.20	–0.349	0.728
U. gallii	2.00	1.29	–1.386	0.166
No. of fledged chicks				
Heather	5.40	3.50	–2.267	0.024
U. europaeus	4.21	3.80	–0.217	0.828
U. gallii	5.29	3.86	–0.982	0.326

$R^2 = 0.72$, $F = 28.20$, $df = 1$, $P < 0.001$). Territories containing *U. gallii* also showed delayed breeding due to disturbance events (Fig. 2: $R^2 = 0.17$, $F = 4.13$, $df = 1$, $P = 0.051$), but the difference between the earliest and latest start times was reduced, around 28 days. *U. europaeus* territories showed no effects of disturbance (Fig. 2: $R^2 = 0.00$, $df = 1$, $F = 0.95$, $P = 0.952$).

Disturbance reduced the overall breeding productivity of territories in all habitat types, but only significantly so in heather-dominated territories (Table 6). Pairs delayed by disturbance events hatched chicks late in the season. They were less likely to fledge young successfully and raised fewer successful broods overall. Because heather territories demonstrated the greatest effects of disturbance, the link between disturbance events and breeding productivity was explored further in subsequent analyses of this habitat type alone. Logistic regression showed that nests located near to the territory edge in high-disturbance areas were significantly more likely to fail than to succeed in fledging young (Fig. 3: $\beta = -0.007$, se = ± 0.003, $df = 1$, $R^2_L = 0.21$. $P = 0.020$, Hosmer & Lemeshof goodness-of-fit test: $\chi^2_8 = 3.456$, $P = 0.903$).

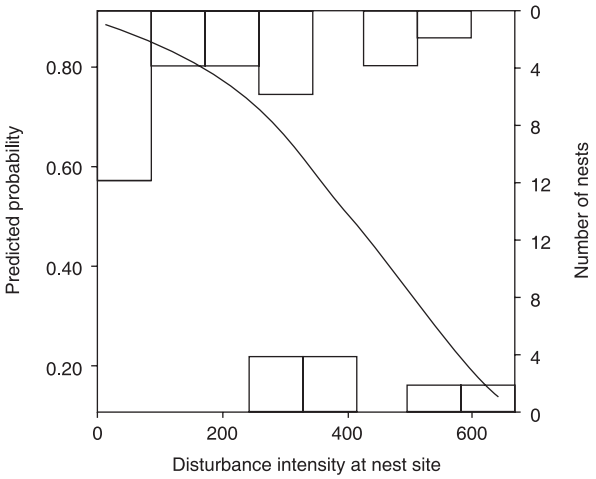

Figure 3. Logistic regression showing the negative relationship between nest outcome (success/failure) in heather territories and disturbance intensity at the nest-site. Disturbance intensity at nests was measured as the distance (metres) from nest-sites experiencing low–high numbers of disturbance events to the edge of the territories. The primary *y*-axis refers to the probability of nest success and the histograms represent the number of nests in each disturbance category for each of the two possible outcomes (nest success/failure).

Mechanisms of disturbance events

There are two likely non-exclusive mechanisms by which disturbance events impact first brood timing and subsequent breeding productivity. One possibility is that hatching dates were delayed, preventing chick growth from coinciding with optimal periods of invertebrate prey density, and thus increasing chick mortality in the nest. Another is that disturbance events acted directly, interrupting adult foraging and chick feeding behaviour. Analyses suggested both processes occurred. To control for effects of disturbance on average hatch dates, data were separated according to hatch date. Heather territory nests that hatched in May and June showed a significant decline in the number of chicks fledged per pair with increasing

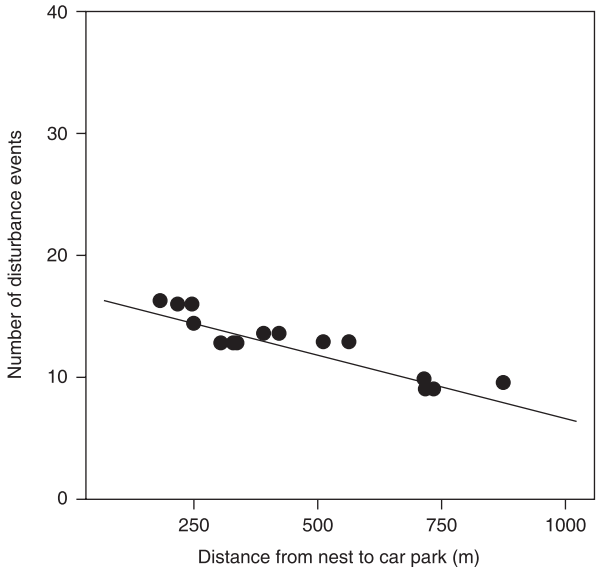

Figure 4. Correlation showing the significant relationship between territory disturbance (number of disturbance events per hour) at heather territories and the distance of nests to the nearest car park.

disturbance intensity ($R^2 = 0.268$, $F = 5.12$, $df = 1$, $P = 0.040$), after controlling for food availability. This implied that some mechanism of disturbance beyond delayed breeding was affecting success, e.g. interference with chick feeding. The productivity of nests hatching in July did not decline with increasing disturbance intensity ($R^2 = 0.118$, $F = 1.07$, $df = 1$, $P = 0.330$), implying that the low productivity of first broods delayed until July was the result of reduced prey availability that month.

In order to investigate further the amount of disturbance required to delay the onset of breeding in heather territories, the relationships between a variety of disturbance factors and nest timing were explored. Proximity of territory centres to the nearest access points showed a strong negative relationship with the timing of first broods ($R^2 = 0.62$, $F = 20.20$, $df = 1$, $P = 0.008$). In nature reserves, where car parks were provided, disturbance at territories was also strongly related to the proximity of parking places available (Fig. 4: $R^2 = 0.834$, $F = 70.33$, $df = 1$, $P < 0.001$). Alternatively, at the more urban sites, which contained mostly *U. gallii* territories, the proximity of access points onto the heath indirectly affected disturbance rates in territories with *U. gallii* ($R^2 = 0.448$, $F = 37.37$, $df = 1$, $P < 0.001$), as did the proximity of surrounding buildings ($R^2 = 0.460$, $F = 39.18$, $df = 1$, $P < 0.001$); the closer the territory centre was to the source of disturbance, the more disturbance events occurred at each territory.

Start times for territories that did not raise a second brood ranged from 16 to 23 May. Entering these dates into regression equations, it was calculated that on average between 13 and 16 disturbance events needed to occur at heather territories each hour every day in order to delay breeding pairs sufficiently to prevent multiple broods. On average, heather territories were exposed to 8.77 ± 5.46 disturbance events per hour, which falls well below the threshold indicated above. However, the number of disturbance events sufficient to preclude second broods does fall within the range experienced by heather-dominated territories and further increases in disturbance may well result in a larger percentage of heather territories failing to raise second broods.

DISCUSSION

Variation among habitats in disturbance impacts

Timing of breeding varied considerably among habitats. Bibby (1977) found a considerable spread in the start dates of nests. For 1975 and 1976, he recorded first egg dates of 15 May ± 9.4 days and 8 May ± 8.4 days, respectively, with differences of 34 and 28 days between first and last start dates in the two years. In 2004, there was a 46-day difference between first and last first-brood nests, in heather-dominated territories, compared with 18 and 26 days in *U. europaeus* and *U. gallii* territories.

Liley and Clarke (2001) found no relationship between the degree of developed land surrounding a heathland and the number of occupying Dartford Warblers, to the extent that restricting public access to a site did not affect bird density. However, van den Berg *et al.* (2001) found weak negative effects of urban/industrial land use on territory choice, above and beyond those caused simply by breeding habitat loss or heathland degradation, which supported the conclusions of previous studies (Catchpole & Phillips 1992, Treweek *et al.* 1998, Haskins 2000). The negative effects of roads on the density of adjacent bird populations have been well documented by Reijnen and Foppen (1994, 1995) and Reijnen *et al.* (1995, 1996), and evidence from van den Berg *et al.* (2001) implies negative impacts from a broader range of human activities. One reason for the variation in findings is that the effects of disturbance may vary depending on the type of habitat occupied by breeding birds.

Although we found no evidence of any direct effect of disturbance at the nest-site including nest damage or predation in this study, recreational disturbance delayed breeding in heather territories, in some cases for up to 6 weeks. Interestingly, it had little effect in gorse territories, in particular those which contained large stands of *Ulex europaeus*. *U. europaeus* provides shelter from harsh weather and protection from predators (Catchpole & Phillips 1992) and as birds often respond to disturbance as they would to potential predators (Finney *et al*. 2005), it may also offer protection from disturbance (Fernandez-Juricic *et al*. 2001).

Breeding territories were always associated with heather. Most contained areas of *U. europaeus* and where sites included *U. gallii* territories were dominated by it to the extent that very little pure heather occurred. First brood timing in *U. gallii* territories showed a weak but still negative relationship with increasing numbers of disturbance events. Delayed breeding pairs produced fewer broods overall. *U. gallii*, unlike *U. europaeus*, offers Dartford Warblers little immediate protection from disturbance. Its growth form is more dense and shorter than *U. europaeus*, possibly too thick to allow effective freedom of movement for birds seeking shelter. However, unlike heather, it is not easy for people and dogs to penetrate *U. gallii*. Dogs were recorded as moving as far as 45 m into heather, but were never seen to move off the path in vegetation dominated by *U. gallii*. Off-path activities have been found to produce more disturbance effects than on-path activities (Miller *et al*. 2001), so it is likely that dogs off-lead had the greatest impact on Dartford Warbler breeding productivity.

Interestingly, previous studies have found that *U. gallii* formed a very small component of Dartford Warbler territories in Dorset (Bibby & Tubbs 1975, Robins & Bibby 1985, Westerhoff & Tubbs 1991, van den Berg *et al*. 2001). There are clear indications from local bird reports (Anon. 1994-2004) and this study that in line with a large increase in the total Warbler population, the numbers found in association with *U. gallii* are increasing. As population size increases, it may benefit from a move into apparently suboptimal habitat as birds here are, overall, less affected by disturbance.

Mechanisms of disturbance impacts

Dartford Warblers proved particularly susceptible to disturbance during the nest-building stage. They are extremely quiet and elusive when nest building and show little sign of alarm if observed (Bibby 1977). Beale and Monaghan (2004) observed that individuals showing little or no response to disturbance might in fact be those with the most to lose from changing their behaviour (see also Gill *et al*. 2001, Gill 2007). When interrupted, Dartford Warblers halted all nest-building activities and any nest material birds might have been carrying was abandoned. This observation agrees with the observations of Nethersole-Thompson (1933), who reported frequent occurrences of disturbance-related nest abandonment during nest building. Incidences of this behaviour were observed on 32 occasions; more than 70% occurred in heather territories. Similarly, observer effects were recorded only at the nest-building stage. We suggest this sensitivity is the prime reason for the delay in raising first broods in heather territories.

High levels of recreational disturbance caused a significant reduction in breeding productivity in heather-dominated territories, by decreasing both the number of successful broods raised and the number of chicks fledged by each breeding pair. The reduced amount of time left for breeding after a delayed start meant potentially fewer successful broods could be raised. It is likely that at those nests in which hatching was delayed to June, fledgling success was reduced both by low densities of insect prey and by disturbance-related interference, which further reduced the foraging effectiveness of birds by keeping adults from the nest for extended periods. First-brood nests that hatched in July did so when invertebrate availability was less than optimal. Other possible causes of reduced breeding productivity might be associated with increased stress (Mullner *et al*. 2004). For example, in heather territories, disturbed breeding birds often became quickly agitated searching for suitable cover, which might result in undetected energetic costs (Stock & Hofeditz 1997).

Our analyses suggest that a minimum of 13–16 people passing through heather territories each hour of every day would delay breeding pairs sufficiently to prevent the production of second or further broods. Disturbed breeding pairs raised fewer successful broods. Nests located close to a territory edge proved more likely to fail outright when exposed to high levels of disturbance. Thus, nests near to the borders of heather territories, located near to access points, proved particularly susceptible to high levels of disturbance. Access points coincide with car parks; car parks were associated with increased numbers of people. Clarke *et al*. (2005) showed that 83% of

dog-walkers do not penetrate further than 1 km onto the heath (see also Underhill-Day & Liley 2007). High numbers of visitors were concentrated around access points to the heathland area.

Reducing the impacts of disturbance

The knowledge that disturbance affects Dartford Warbler breeding productivity differently across habitats is of particular applied importance. Specifically, heather territories located adjacent to open recreational areas such as lawns, access points and car parks require special attention. Visitor access to such areas can be manipulated by the appropriate location of gates, car parks and footpaths, and at some sites by restricting the nature of access (such as putting dogs on leads), or assigning areas protected status by limiting path access and creating footpath diversions during the breeding season. Habitat manipulation is also a possible means of countering disturbance effects. Planting *U. europaeus* in heather-dominated territories exposed to high levels of disturbance could offset some of the effects of recreational disturbance by providing the necessary cover, as well as screening or restricting penetration into heather from adjoining paths, although this might conflict with other conservation aims. The effectiveness of access management techniques such as these warrants further study.

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REFERENCES

Anderson, R., Linnell, J.D.C. & Langvatn, R. 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. *Biol. Conserv.* **77**: 169–176.

Anon. 1994–2004. *Dorset Bird Reports*. Dorset Bird Club.

Bathe, G. 2001. *Countryside and Rights of Way Act 2000. A User's Guide*. Unpublished report. Peterborough, UK: English Nature.

Bathe, G. 2007. Political and social drivers for access to the countryside: the need for research on birds and recreational disturbance. *Ibis* **149** (Suppl. 1): 3–8.

Beale, C.M. & Monaghan, P. 2004. Behavioural responses to human disturbance: a matter of choice? *Anim. Behav.* **68**: 1065–1069.

van den Berg, L.J.L., Bullock, J.M., Clarke, R.T., Langston, R.H.W. & Rose, R.J. 2001. Territory selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role of vegetation type, habitat fragmentation and population size. *Biol. Conserv.* **101**: 217–228.

Bibby, C.J. 1977. *Dartford Warblers in Britain*. PhD thesis, RSPB/Institute of Terrestrial Ecology.

Bibby, C.J. 1978. Conservation of the Dartford Warbler on English lowland heaths. *Biol. Conserv.* **13**: 299–307.

Bibby, C.J. 1979a. Foods of the Dartford warbler *Sylvia undata* on southern English heathland. *J. Zool., Lond.* **188**: 557–576.

Bibby, C.J. 1979b. Mortality and movements of Dartford Warblers in England. *Br. Birds* **72**: 10–22.

Bibby, C.J. & Tubbs, C.R. 1975. Status, habitats and conservation of the Dartford Warbler in England. *Br. Birds* **68**: 177–195.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. 2000. *Bird Census Techniques*. London: Academic Press.

Bullock, J.M., Edwards, R.J., Carey, P.D. & Rose, R.J. 2000. Geographical separation of two *Ulex* species at three spatial scales: does competition limit species' ranges? *Ecography* **23**: 257–271.

Burger, J., Gochfeld, M. & Niles, L.J. 1995. Ecotourism and birds in coastal New Jersey: contrasting responses of birds, tourists and managers. *Environ. Conserv.* **22**: 56–65.

Carney, K.M. & Sydeman, W.J. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* **221**: 68–79.

Catchpole, C.K. & Phillips, J.F. 1992. Territory quality and reproductive success in the Dartford Warbler *Sylvia undata* in Dorset, England. *Biol. Conserv.* **61**: 209–215.

Clarke, R., Liley, D., Underhill-Day, J. & Rose, R. 2005. *Visitor access patterns on the Dorset heathlands*. English Nature Research Report. Peterborough, UK: English Nature.

Cramp, S. (ed.) 1992. *The Birds of the Western Palearctic*, Vol. 6. Oxford: Oxford University Press.

Fernandez-Juricic, E., Jimenez, M.D. & Lucas, E. 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environ. Conserv.* **28**: 263–269.

Field, A. 2000. *Discovering Statistics Using SPSS for Windows*. London: Sage Publications.

Finney, S.K., Pearce-Higgins, J.W. & Yalden, D.W. 2005. The effect of recreational disturbance on an upland breeding bird, the golden plover *Pluvialis apricaria*. *Biol. Conserv.* **121**: 53–63.

Frid, A. & Dill, L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* **6**: Article number 11.

Gibbons, D.W. & Wotton, S. 1996. The Dartford Warbler in the United Kingdom in 1994. *Br. Birds* **89**: 203–212.

Gill, J.A. 2007. Approaches to measuring the effects of human disturbance on birds. *Ibis* **149** (Suppl. 1): 9–14.

Gill, J.A., Sutherland, W.J. & Watkinson, A.R. 1996. A method to quantify the effects of human disturbance on animal populations. *J. Appl. Ecol.* **33**: 786–792.

Gill, J.A., Norris, K. & Sutherland, W.J. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biol. Conserv.* **97**: 265–268.

Goodrich, J.M. & Berger, J. 1994. Winter recreation and hibernating black bears *Ursus americanus*. *Biol. Conserv.* **67**: 105–110.

Haskins, L.E. 2000. Heathlands in an urban setting – effect of urban development on heathlands of south-east Dorset. *Br. Wildl.* **11**: 229–237.

Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R. & Treweek, J. 1997. Bird disturbance: improving the quality and utility of disturbance research. *J. Appl. Ecol.* **34**: 275–288.

Hockin, D., Ounsted, M., Gorman, M., Hill, D., Keller, V. & Barker, M.A. 1992. Examination of the effects of disturbance on birds with reference to its importance in ecological assessments. *J. Environ. Manage.* **36**: 253–286.

Liley, D. 1999. *Predicting the Consequences of Human Disturbance, Predation and Sea-level Rise for Ringed Plover Populations*. PhD thesis, University of East Anglia.

Liley, D. & Clarke, R.T. 2001. *Urban Development Adjacent to Heathland Sites in Dorset: the Effect on the Density and Settlement Patterns of Annex I Bird Species*. Report for public enquiry. Poole: RSPB/CEH.

Liley, D. & Sutherland, W.J. 2007. Predicting the population consequences of human disturbance for Ringed Plovers *Charadrius hiaticula*: a game theory approach. *Ibis* **149** (Suppl. 1): 82–94.

Miller, S.G., Knight, R.L. & Miller, C.K. 2001. Wildlife responses to pedestrians and dogs. *Wildl. Soc. Bull.* **29**: 124–132.

Moore, N.W. 1962. The heaths of Dorset and their conservation. *J. Ecol.* **50**: 369–391.

Mullner, A., Linsenmair, K.E. & Wikelski, M. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biol. Conserv.* **118**: 549–558.

Nethersole-Thompson, D. 1933. The field habits, and nesting of the Dartford Warbler. *The Oologist's Record* **13**: 51–61.

Reby, D., Cargnelutti, B. & Hewison, A.J.M. 1999. Contexts and possible functions of barking in roe deer. *Anim. Behav.* **57**: 1121–1128.

Reijnen, R. & Foppen, R. 1994. The effects of car traffic on breeding bird populations in woodlands. I. Evidence of reduced habitat quality for Willow Warblers (*Phylloscopus trochilus*) breeding close to a highway. *J. Appl. Ecol.* **31**: 85–94.

Reijnen, R. & Foppen, R. 1995. The effects of car traffic on breeding bird populations in woodland. IV. Influence of population size on the reduction of density close to a highway. *J. Appl. Ecol.* **32**: 481–491.

Reijnen, R., Foppen, R., ter Braak, C. & Thissen, J. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction in the density in relation to the proximity of main roads. *J. Appl. Ecol.* **32**: 187–202.

Reijnen, R., Foppen, R. & Meeuwsen, H. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biol. Conserv.* **75**: 255–260.

Robins, M. & Bibby, C.J. 1985. Dartford Warblers in 1984 in Britain. *Br. Birds* **78**: 269–280.

Rose, R.J., Webb, N.R., Clarke, R.T. & Traynor, C.H. 2000. Changes on the heathlands in Dorset, England, between 1987 and 1996. *Biol. Conserv.* **93**: 117–125.

Smart, J., Sutherland, W.J., Watkinson, A.R. & Gill, J.A. 2004. A new means of presenting the results of logistic regression. *Bull. Ecol. Soc. Am.* **85**: 100–102.

Stock, M. & Hofeditz, F. 1997. Compensatory limits: energy budgets of Brent Geese, *Branta bernicla*, the influence of human disturbance. *J. Ornithol.* **138**: 387–411.

Treweek, J.R., Hankard, P., Roy, D.B., Arnold, H. & Thompson, S. 1998. Scope for strategical ecological assessment of trunk road development in England with respect to potential impacts on lowland heathland, the Dartford warbler (*Sylvia undata*) and the sand lizard (*Lacerta agilis*). *J. Environ. Manage.* **53**: 147–163.

Underhill-Day, J.C. & Liley, D. 2007. Visitor patterns on southern heaths: a review of visitor access patterns to heathlands in the UK and the relevance to Annex I bird species. *Ibis* **149** (Suppl. 1): 112–119.

Webb, N.R. & Haskins, L.E. 1980. An ecological survey of heathlands in the Poole Basin, Dorset, England in 1978. *Biol. Conserv.* **17**: 281–296.

Weimerskirch, H., Shaffer, S.A., Mabille, G., Martin, J., Boutard, O. & Rouanet, J.L. 2002. Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation, and the effects of human disturbance. *J. Exp. Biol.* **205**: 475–483.

Westerhoff, D. & Tubbs, C.R. 1991. Dartford warblers *Sylvia undata*, their habitat and conservation in the New Forest, Hampshire, England in 1988. *Biol. Conserv.* **56**: 89–100.

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