BEHAVIOURAL RESPONSES OF PARK RED AND FALLOW DEER TO DISTURBANCE AND EFFECTS ON POPULATION PERFORMANCE

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Abstract

Within two London parks, Richmond and Bushy, both subject to high public visitor pressure, behavioural observations were undertaken to investigate patterns of habitat use by red and fallow deer populations, and to determine the response of the deer to human disturbance. Potentially disturbing events were considered as: i. people present within a distance of < 50m; ii. people present within 50m accompanied by a dog on a lead; iii. dogs within 50m off the lead; iv. people 'crowding' the deer - approaching directly and deliberately for photographs or closer observation; v. actual chases by a dog of the deer group or a member of that group.

All the above levels of disturbance caused a measurable change in the immediate behaviour patterns of the deer - reflected in increased levels of vigilance. Females responded more strongly than males of either species. However, the effects were relatively minor and transient in the great majority of cases, with animals resuming their normal activity very quickly after the encounter.

Overall daily time-budgets did not differ significantly between undisturbed days and days when disturbance levels were high; nor were any effects apparent on patterns of habitat use by the deer or in forcing the animals to change habitat more frequently. Further, throughout our studies there was no evidence that levels of disturbance caused by public access had any deleterious effects on body-weights or overwinter mortality.

Keywords: *animal welfare, deer parks, disturbance, fallow deer, population performance, red deer*

Animal welfare implications

There has been considerable recent concern about the consequences of human recreational activity on behaviour and welfare of deer in public parks. This paper reports the results of an extensive study of the levels of public disturbance experienced by red and fallow deer in two London parks, behavioural responses to that disturbance, and an analysis of the effects of chronic disturbance on population performance. We could show no significant effects of disturbance on daily time-budgets of either red or fallow deer, nor

on patterns of habitat use by the deer. Further, throughout our studies there was no evidence that levels of disturbance caused by public access had any deleterious effects on body-weights or overwinter mortality. Overall, effects of disturbance on the behaviour of the deer were thus found to be slight or transitory, and of only minor importance with regard to long term consequences on their performance.

Introduction

There has been a great deal written in recent years about the potential influence of human disturbance and recreational activity on wildlife; yet in practice - while a good deal is known of the effects of trampling damage, soil compaction and erosion on vegetation (review by Liddle 1991), far less objective data are available on the effects of disturbance on animal populations, particularly among mammals. Some limited material is available from the USA on the effects of snowmobiles, snow scooters and direct approach by humans on foot, on escape reactions of white-tailed deer and moose (Freddy *et al* 1986), and Tyler (1991) has assessed the energetic costs to Svalbard reindeer of human activities. Within Europe too there have been a number of publications addressing this issue (eg Hartfiel *et al* 1985) but in the main such material has been largely anecdotal. Isolated pieces of objective data may be gleaned from various (often unpublished) sources but these are rarely offered in the context of a complete analysis. Thus a report prepared for the Swedish Orienteering Federation (SOF no date) presents detailed observations on the responses to orienteering events of 40 roe deer and 25 moose equipped with radiotelemetric transmitters. All of the moose in the survey area moved quickly out of the area of disturbance, travelling distances of between 5-10km; all had however returned to their home territories within a few days. Roe deer disturbed by the event were less likely to leave their home ranges, only travelling distances of 1 km (females) or 1.8 km (males) and returning to their normal ranges within a day (see also Jeppesen 1987). This report further notes that none of the animals monitored were found dead or injured after the orienteering events observed; neither were they found in conditions of stress during the competition itself, although anecdotal reports of stress-death amongst moose during such events had previously been recorded (SOF no date). Similar results were reported from a study of the effects of orienteering events on wildlife in the New Forest in southern England, assessing behaviour, flight responses and return times of fallow deer disturbed along the route (Douglas 1991).

More recently there has been a series of publications within the UK suggesting that disturbance from human activities might be implicated in sudden and unexpected 'die-offs' among populations of park deer. Thus when, at the end of the 1985/6 winter, 13 per cent of the population of red and fallow deer in Richmond Park, London, were found dead or dying of unknown causes, this was tentatively attributed by park managers to the cumulative effects of disturbance within the park. Likewise, early published reports of a series of heavy mortalities associated with infection by *Pasteurella multocida*, amongst the fallow deer population of Dunham Massey Park, near Manchester, tentatively suggested that such infections had been triggered by stress due to disturbance (Lawton

1987). Since such reports a number of studies have investigated more specifically the effects of human activity on behaviour of deer in public parks (Humphries *et al* 1989, Bullock *et al* 1990, in press). These again suggest a direct effect of human disturbance on social behaviour and activity budgets of red and fallow deer and imply that chronic and repeated disturbance may be expected to have long term effects on population performance.

This paper presents the results of a long term study of the behaviour of both red and fallow deer in two London parks of high public use and an analysis of the effects of human activity within the parks on habitat use and activity patterns of the deer. In addition, results are presented from a more extensive survey of population performance in a number of British deer parks subjected to different levels of public access; these allow us to investigate any possible correlations between levels of disturbance and mortality, reproductive success, growth rates and adult body-weights. We would note that these later analyses include both Richmond and Dunham Massey parks, the two parks where heavy mortalities have previously been attributed to the effects of disturbance.

Methods

Patterns of habitat use, activity budgets and behavioural response to disturbance

Data collection on the behaviour of red and fallow deer and their response to disturbance focused on the two Royal parks of Richmond and Bushy. Both parks are situated in south-west London within 12 km of the city centre and are open to the public throughout the year. The sites have similar vegetation of open parkland character. In both parks *c* 60 per cent of the total area consists of managed pasture with scattered mature trees, with 20 - 30 per cent of rougher, tussocky grassland or stands of bracken. Woodland accessible to the deer contributes a further 18 per cent of the total area in Richmond; less woodland (3.5%) is available to the deer in Bushy park.

Both parks support mixed populations of red and fallow deer at similar stocking densities; average overwinter numbers during the period of study were: Richmond, 393 fallow and 343 red deer (on 820 ha); Bushy, 191 fallow, 170 reds (on 385 ha).

In both sites, data on the behaviour of the animals were collected by two, complementary methods: observations of habitat use patterns were made during transect surveys of the instantaneous distribution and habitat occupance of the main body of the deer population within the park; data on time-budgets and behavioural response to disturbance were collected during 'follows' of individual deer or groups of particular sex/ species.

Habitat use transects

Regular transect routes were established in each of the two parks to allow the observer to survey as large a proportion of the total area of the park as possible and to cover all different habitat types available to the deer. In Richmond, the route extended some 11 miles (17.7km) and effectively sampled 75 - 90 per cent of the total park area, depending

on the differential visibility of different seasons; in Bushy Park, a transect of 4 - 5 miles (6.4 - 8km) allowed the observer to survey 80 per cent of the entire park. Transects were traversed slowly by car, stopping each time a group of animals was encountered to record the number of animals in the group by sex and species, habitat(s) occupied, activity and location. Each transect took approximately 1-1.5 hours to complete (depending on traffic and animal activity); at the beginning and end of each survey a note was made of temperature, cloud cover and general weather conditions, and readings of wind speed at a constant position on a hand-held flow meter.

From 2 - 4 transects were undertaken on any one day, spread through the daylight hours to ensure even coverage of the entire period. Transect surveys were repeated, on average, on eight days per month in Richmond, and four days per month in Bushy, from October 1988-March 1990. Broad habitat categories were distinguished as:
1. areas of good pasture, in the open, or associated with trees (parkland); 2. areas of rough grassland, once again, in the open or associated with scattered mature trees (parkland with rough grazing); 3. woodland areas, 4. stands of bracken, *Pteridium aquilinum*.

Focal animal observations
Data on the behaviour of the animals and their responses to disturbance were collected during follows of target groups of deer. During such follows, a group of deer was located at random within the park at the beginning of a day's sampling. Contact was thereafter maintained with that group for as long as possible. A focal animal was selected within the group - an animal whose identity could be recognized by some distinguishing feature throughout the watch. Records were made every 10 minutes of the activity of this focal animal, using binoculars or a spotting telescope; observations were made from a parked car or from a concealed position 100-150 metres from the focal group. Behaviours were recorded as feeding, lying, standing calm, standing vigilant or on the move, and the habitat occupied. An animal was considered by us as vigilant if it was standing alert, with head above the horizontal, clearly attentive and scanning the immediate area. Focal animal data were supplemented by scan surveys of the rest of the group on the same recording interval noting total number of individuals in the group by species and sex, and behaviour of each. Where groups split or amalgamated during the watch, the observer remained with that part of the group containing the focal animal.

On average watches lasted 4.5 hours (range 3 - 7.5 hours) and contact with the animals was usually maintained over a period between 0800 and 1600h or between 1100 and 1800h. Throughout the watches, records were made of weather conditions and the incidence of any potentially disturbing event (human walking past, human approaching, dog on lead, dog off lead etc) at the instant of the 10 minute behavioural recording and the total number of such instances in the 10 minute period preceding that record. Potentially disturbing events were considered as:

1. people present, either standing still or walking past, within a distance of < 50m;
2. people present within 50m accompanied by a dog on a lead;

3. dogs within 50m off the lead;
4. people 'crowding' the deer - approaching directly and deliberately for photographs or closer observation;
5. those instances where a dog actively chased the group or a member of that group.

Separate follows were undertaken in each month focusing on red stags, red hind groups, fallow bucks and fallow does and followers. Three days' of observation of each type of group was undertaken every two months in Richmond between October 1988 and December 1989; in Bushy, level of sampling intensity was reduced, with one follow per month devoted to each of the four classes of deer, for purposes of comparison. A total number of 187 hours of follows were undertaken in Richmond over a 14-month period (although on occasions, records could be maintained on two focal individuals simultaneously during such watches). Seventy-six hours of follows were carried out in Bushy Park.

Statistical analysis

Behavioural reaction, of individuals or groups of deer, to different types of disturbance was assessed through comparisons of the number of occasions when challenged by each disturbance type (or when undisturbed). The focal individual under observation was recorded as vigilant or on the move - or in analysis of group data, >10 per cent of the group were alert or moving. Comparisons were made by Fisher's Exact test, or the G-test for homogeneity where appropriate (Sokal & Rolff 1981). Variation in overall time-budgets of the deer due to season, and differences in allocation of time to different activities on days of high or low public disturbance, were also compared using the G-test.

Analyses of the effects of human activity on patterns of habitat use by the deer were carried out using multiple analyses of variance on transformed data. Habitat use data were recorded throughout as actual numbers of deer seen in each habitat type during transect surveys. Such data represent quantitative numerical values rather than true frequencies; further, with a finite number of deer present in the park, values recorded in each habitat are not strictly independent. In statistical analyses of these data we therefore used the additive logistic transformation (Aitchison 1982, and quoted by Wilkinson 1986). In this transformation n+1 original variables, x_i are converted to n new variables, y_i as $y_i = \ln(x_i / x_{i+1})$. In our case, all records of animals seen in each habitat type in any transect are divided through by the number of records in the most commonly used habitat type (good grazing) and then logged. The new variable set contains all the information of the old and each variable is now approximately normally distributed and independent of the others. Statistical analyses of these transformed variables were then carried out using Multivariate Analysis of Variance (MANOVA) with the SPSSX statistical package. The analysis used a one-way design, using proportional occupance of different habitats as multiple dependent variables, to test the effects of a single categorical variable, disturbance level, on differences in the pattern of use of the various habitats.

Table 1 Rates with which different types of potentially disturbing events were encountered by deer observed at Richmond and Bushy parks.

All such potentially disturbing events occurring in the vicinity of the focal group of deer throughout any observation period were recorded and are included in calculation of the encounter-rates shown. Weekends include holidays.

RICHMOND

Daytime hours observed			Potentially disturbing events per hour					
			Type 1	Type 2	Type 3	Type 4	Type 5	Total
Winter:	*weekdays*	35.3	1.87	0.08	0.96	0.11	0.03	3.06
	weekends	11.2	3.13	0.09	1.97	0.45	0.00	5.64
	total	46.5	2.17	0.09	1.20	0.19	0.02	3.68
Spring:	*weekdays*	64.3	2.07	0.53	1.45	0.09	0.00	4.13
	weekends	9.7	1.86	0.00	1.03	0.41	0.00	3.31
	total	74.0	2.04	0.46	1.39	0.14	0.00	4.03
Summer:	*weekdays*	40.5	2.20	0.12	1.33	0.25	0.00	3.90
	weekends	7.0	4.57	0.86	2.00	0.57	0.00	8.00
	total	44.0	2.39	0.18	1.39	0.27	0.00	4.23
Autumn:	*weekdays*	11.5	1.04	0.00	1.04	0.52	0.00	2.61
	weekends	10.7	11.63	0.66	1.03	4.78	0.00	18.09
	total	22.2	6.14	0.32	1.04	2.57	0.00	10.06

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Winter:	*weekdays*	11.5	1.22	0.35	1.22	0.09	0.00	2.87
	weekends	-	-	-	-	-	-	-
	total	11.5	1.22	0.35	1.22	0.09	0.00	2.87
Spring:	*weekdays*	18.2	4.02	0.83	1.54	0.28	0.06	6.72
	weekends	9.2	1.53	0.44	0.98	0.11	0.00	3.05
	total	27.3	3.18	0.70	1.35	0.22	0.04	5.49
Summer:	*weekdays*	15.8	2.21	0.44	1.71	0.13	0.13	4.61
	weekends	6.7	1.65	0.15	1.05	0.00	0.30	3.15
	total	22.5	2.04	0.36	1.51	0.09	0.18	4.18
Autumn:	*weekdays*	5.2	3.87	0.19	2.90	0.00	0.00	6.97
	weekends	9.8	5.69	0.92	3.86	0.00	0.10	10.58
	total	15.0	5.07	0.67	3.53	0.00	0.07	9.33

Key to disturbance types distinguished

Type 1 : person walking past or standing within < 50m; Type 2 : person with dog on the lead within < 50m; Type 3 : person with dog **off** the lead within < 50m; Type 4 : deliberate close approach by people; Type 5 : dog chase

Results

Immediate response to disturbance

The frequency with which deer under observation were challenged by the different types of potential disturbance recognized - and the encounter-rate (as number of interruptions per hour) are tabulated in Table 1. Based on these figures, both parks seem to share broadly similar patterns of disturbance. Deleterious effects of such disturbance could result from disruption of ongoing behaviour, or enforced habitat change, forcing cessation of feeding, or driving the animals out of cover where they might have gone to escape extremes of weather conditions.

Effects on habitat occupance

In considering the possible effects of disturbance on patterns of habitat use, we regressed the number of changes of habitat per hour recorded for groups of deer against the total encounter-rate of different levels of disturbance over the same period. Rates of change of habitat ranged from 0 - 0.9 per hour; encounter-rates with disturbance over the same watches ranged from 0-29 per hour. No significant relationship between rate of habitat change and disturbance could be detected. Indeed, disturbance explained only 0.79 per cent of the observed pattern of habitat change in Bushy Park and only 5.3 per cent in Richmond Park.

In those changes of habitat recorded during follows which did coincide with some measure of current disturbance, we examined the data further to see whether, when such changes did occur these were consistently forcing animals from closed into open areas or from feeding grounds into cover. As such events were rare, data were pooled for both deer species and analyses were undertaken over the year as a whole. Results are presented in Table 2 which shows for each park the number of habitat changes which coincided with an actual **current** disturbance at the time of change. Note that the animals may have been going to shift habitats at this time anyway and in no case is there incontrovertible evidence that these changes were necessarily connected with the simultaneous disturbance. The table reinforces the impression that many encounters with potential disturbances are not accompanied by a change in habitat. Only limited data were available for animals encountering disturbance within cover and these are not considered further here; of 26 occasions when disturbance did coincide with a change in habitat for animals which were at the time in the open, 24 such changes were to other open communities and only two involved a shift to cover.

Effects on immediate behaviour

To investigate the immediate effects of disturbance on behaviour and to assess the strength of response to different types of disturbance, we considered the response of focal individuals and of groups to disturbances of different magnitude.

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Table 2 Movement between vegetation-types in relation to disturbance. Data are combined for both sexes/species and are reviewed over the year as a whole. Closed habitat types include woodland and bracken areas; open include good or rough grazing with or without parkland trees.

RICHMOND

Animals initially observed	in closed habitat						in open habitat					
Disturbance type	**1**	**2**	**3**	**4**	**5**	**Total**	**1**	**2**	**3**	**4**	**5**	**Total**
Disturbances encountered	6	0	8	1	1	16	103	16	42	36	3	200
Co-incident with habitat change	2	0	0	0	0	2	6	1	2	8	0	17
Change: closed to open	2	0	0	0	0	2						
open to closed							1	0	1	0	0	2

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Disturbances encountered	(insufficient data)						40	7	43	5	2	97
Co-incident with habitat change							4	1	2	2	0	9
Change: open to closed							0	0	0	0	0	0

On each occasion during a follow where some measure of disturbance actually coincided with the record of the behaviour of the focal individual (taken on the 10th minute), the animal was scored as having responded to the disturbance if the behaviour recorded showed it vigilant or on the move, but not to have reacted if it remained calm, continued feeding or lying. For group data, a group was considered to have responded if more than 10 per cent of the animals within that group were scored as vigilant or on the move. Animals may display some measure of alertness, or move for reasons other than immediate disturbance (they may just be looking around them or moving from one feeding patch to another); to offer some sort of control for these data on response to disturbance therefore, we also noted the number of times a focal animal (or>10% of a given group) was recorded as alert or moving when it was **not** disturbed - and no disturbance had occurred within the entire previous 10 minute period. Because of the high level of movement recorded for males during the autumn rut, observations on male deer during this period are omitted from the analyses.

Data are presented in Table 3; here, 0=no disturbance and other codes are as before. We note however that dog chases are now pooled with category 3 (dogs off lead) in statistical analyses. Results of Table 3 show clearly that the deer do show some measure of reaction to all those types of encounter we have considered as potentially disturbing. Apart from stags which showed no significant change in their degree of vigilance or movement in response to any type of disturbance, all the three other classes of deer at

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Richmond showed significant increase in vigilance for all types of disturbance. In analysis of group data, the frequency of occasions when more than 10 per cent of the group were recorded as vigilant or on the move was significantly higher even with our lowest category of disturbance (people within 50m; Fisher's Exact test: $p<0.01$ in all cases) than when the group had experienced no challenge for 10 minutes. Proportion of the group vigilant or on the move increased still further over that of undisturbed groups for dogs off the lead (category 3) and for crowding by people (category 4; sufficient data only available for hinds and does: $p<0.005$ in all cases).

Table 3 Behavioural responses to disturbance of groups and individuals.

Figures show the number of times a group of deer or a focal individual encountered a particular type of disturbance, and record how often it did or did not react. Reaction for the individual is defined as those occasions when the animal moved or stood vigilant. Groups were considered to react if more than 10% of the group were recorded as vigilant or on the move after the disturbance. Group data include figures for occasions when > or < 10% of the group were vigilant without any disturbance '0' having occurred in the previous 10 minutes.

RICHMOND

		Group						Focal individual				
Disturbance type		**0**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Bucks	*Non-react*	98	11	0	8	1	0	14	1	11	1	0
	React	10	5	1	5	0	0	0	0	2	0	0
Does	*Non-react*	209	26	3	4	4	0	29	6	7	10	0
	React	33	11	4	7	8	1	2	2	3	3	0
Stags	*Non-react*	94	14	3	14	1	0	16	3	16	2	0
	React	14	1	0	3	1	0	0	0	0	0	0
Hinds	*Non-react*	155	17	1	1	2	0	26	1	11	4	0
	React	28	10	0	8	4	0	2	0	2	1	0

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Bucks	*Non-react*	48	4	2	6	0	0	5	3	7	0	0
	React	6	1	1	3	1	1	0	0	1	0	0
Does	*Non-react*	55	6	0	5	0	0	7	1	6	1	0
	React	6	1	0	1	1	0	0	0	1	0	0
Stags	*Non-react*	36	4	0	3	0	0	5	0	4	0	0
	React	3	2	0	1	0	0	1	0	0	0	0
Hinds	*Non-react*	82	9	2	5	1	0	11	2	8	2	0
	React	5	3	1	7	2	1	1	1	3	1	1

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Data for Bushy Park showed similar patterns; sample sizes were too small for formal statistical analysis except to confirm that here, too, red hinds respond even to the slight level of disturbance of people passing (frequency of >10% of the group vigilant or on the move greater than that of undisturbed groups: $p<0.02$).

Note however, that although in both parks a significant increase in vigilance or movement could be detected in response to disturbance, that increase was relatively slight and the most common response observed from both individuals and groups in the majority of encounters was ***non-reaction****, even at the highest levels of disturbance.*

Group data were explored further in an analysis of differences in the frequency of response (>10% vigilant or on the move) to different types of disturbance. In Bushy Park instances of disturbance above the level of people passing, with or without dogs on the lead, were rather few and provided insufficient data at these higher levels of disturbance to permit us to compare responses. In Richmond, data sets were more robust. Groups of does were recorded with >10 per cent vigilant or on the move on a far greater proportion of those occasions when they were crowded by people than of those occasions when merely passed by humans within 50m (Fisher's Exact test: $p<0.05$); again however, note that this is an increase to a level where 50 per cent of the groups contain >10 per cent animals alert, from a base level, without disturbance, of *c* 15 per cent - and many groups still fail to show any reaction of alarm. Probability of response to dogs off the lead was also higher than that for humans within 50m ($p<0.05$). Results for red hinds were similar to those of fallow does, but neither stags nor bucks showed a significant difference in their degree of response to different levels or types of disturbance.

It is striking that in both cases females responded more positively to any given potential challenge than did males. Group data were pooled for Richmond and Bushy to explore this further. Throughout, groups of hinds were more likely to exceed our threshold of >10 per cent responding than were groups of stags (response to people within 50m, difference $p<0.1$; categories 3 or 4: $p<0.001$; response to all disturbance irrespective of type: $p<0.001$) and females overall (does and hinds combined) responded more frequently than male deer. (Response to humans within 50m again just missing significance at $p<0.1$; dogs off lead or people crowding: $p<0.001$; all types of disturbance pooled: $p<0.001$).

Necessarily, data based on observations of focal individuals are less extensive, but it is clear from the table that results from individual observations closely reflect group data. Deer are more likely to be recorded as vigilant or on the move in the face of some current experience of disturbance than if they are undisturbed and their response is heightened to crowding by people or dogs off the lead. There is one important further point we should note however. Although individual deer **are** more likely to become vigilant or move in response to disturbance, as individuals they respond far less frequently than a response might be noted from the group of which they are a part. That is, a given challenge will far more frequently result in a proportion in excess of 10 per cent of any group being vigilant or moving than it will affect any given individual within that group; not every event which evokes a group response will necessarily affect any

given individual within that group.

Statistical exploration of this data confirms that the frequency with which any individual responds to a challenge encountered by its group is significantly lower than the frequency with which some response will be observed within the group as a whole. Fisher's Exact test, applied to the frequency of response to disturbance (all categories) by a focal individual and the group as a whole showed far greater likelihood of a response observed from the group to any given challenge than that the focal individual itself should be disturbed (stags: $p<0.05$; hinds: $p<0.001$; bucks: $p<0.02$; does: $p<0.002$). Although perhaps obvious, the magnitude of difference between group and individual response emphasizes that any estimate of the frequency with which deer are disturbed which is based on observations of groups rather than actual individuals will **significantly over-estimate** the frequency with which behaviour is disrupted.

Effects of disturbance on activity and time-budgets

Noting that the deer **did** show some instantaneous change in behaviour in response to disturbance, we investigated what might be the long term consequences of such disruption of ongoing behaviour in relation to the overall time-budget expressed. During follows, behaviour of the focal individual animal and the surrounding group was recorded in five simple, exclusive categories: animals were scored as feeding, lying down, on the move, standing calm and standing vigilant.

The percentage of time spent in each activity is summarized in Figure 1 for each sex of the two species of deer in Richmond Park by way of example; results are presented by season and record the proportion of time spent in each activity by the focal animal of the watch. In both Richmond and Bushy parks activity patterns recorded in autumn for all classes of deer: males **and** females, were significantly different from those of other seasons (G-test: $p<0.001$). By contrast, no differences could be detected for any sex/species between winter, spring and summer. Excluding the period of the autumn rut, activity patterns for both sexes and both species of deer were thus very similar throughout the year and broadly similar in both parks. Deer of all classes, bucks and does, stags and hinds, spent the bulk of their time feeding or resting (lying). Fallow bucks and does appeared to spend more of their time standing calm during winter than at other times but these differences were not statistically significant. From both focal animal and group data, male deer in both parks seem to spend more time lying in the better weather of spring and summer than in the winter; fallow does perhaps spend slightly more time feeding over the same period.

To investigate possible effects of disturbance on activity budgets, we next calculated separate daily time-budgets for each species and sex for days when the deer experienced a high level of disturbance and those when they were relatively undisturbed. We divided the records into those observation periods in which encounter-rate by the deer with any type of potential disturbance remained low, below 2.5 per hour, those where encounters with people or their dogs were intermediate, between 2.6 - 3.9, and those where levels of encounter exceeded 4.0 per hour.

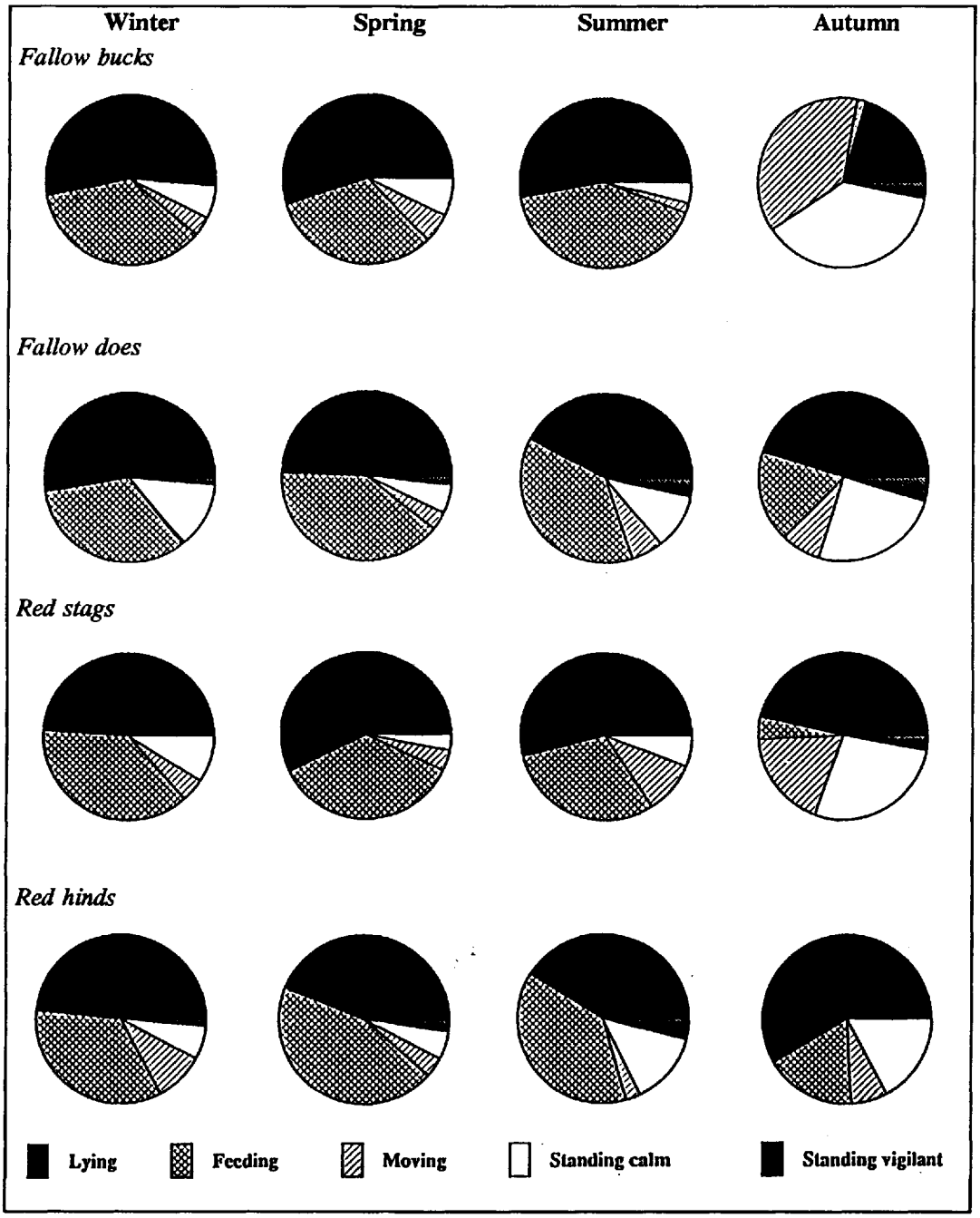

Figure 1 Activity budgets of red and fallow deer in Richmond Park. Figure shows proportion of time spent in different activities by stags, hinds, bucks and does in each of four seasons.

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Records for the two species of deer and the different sexes were kept distinct, but, since few significant differences were detected between the time-budgets of different seasons, excepting those of autumn, records for winter, spring and summer were pooled. Comparisons were carried out by G-test for homogeneity (see Methods section).

No differences in the overall daily time-budgets of red or fallow deer of either sex could be detected in Bushy Park in relation to levels of disturbance experienced during the follow. In Richmond differences during winter, spring and summer were detected only for the behaviour of red stags, which spent slightly less time feeding and more time lying down on days when levels of disturbance were high. During the autumn, at Richmond, fallow bucks spent more of their time standing calm on days of higher than average disturbance and spent less time lying down; there was no difference in the amount/proportion of time spent vigilant or on the move and in fact the increase in time standing calm precisely balanced the decrease in time spent lying down. Effectively the animals remained calm and at rest, but spent the time they would normally have spent lying down, standing.

Effects of human activity on overall patterns of habitat use

Data from transect surveys of the two parks can be used in analysis of the relative use made by the deer over a longer time scale of different vegetational types, and seasonal differences in such patterns of habitat use.

Seasonal changes in patterns of habitat use and differences between the species and sexes of deer in patterns of habitat use expressed, are described in more detail elsewhere (Putman & Langbein 1991b). In essence, in both parks, males and females of both species spend >50 per cent of their time in all seasons on open grazing areas. Of all classes of deer, fallow does tend to concentrate most markedly on areas of good grazing; bucks make more use of rough grazing areas and red deer of both sexes greater use still of these areas of rougher pasture. There is a clear seasonal change in the pattern of use of different habitats, with deer in Richmond making more extensive use of woodland and rough grazing areas (particularly those associated with parkland) during winter or during periods of bad weather at any time of year. With much less woodland available at Bushy animals increase overall their use of parkland rough grazing over the same periods. (Measurements of wind speed in different cover types show that those cover types selected in bad weather achieved a reduction in effective wind speeds experienced by sheltering animals of up to 50 - 80%).

Our main focus in this paper is a consideration of the effects of human disturbance on such behaviour patterns. We considered the effects of different levels of public access on patterns of habitat use shown by the deer, by comparing results of transects conducted on weekdays with those at weekends or holidays, and comparing results from individual transects carried out at times when use of the main car parks was low (fewer than 25 cars), medium or high (>85 cars) in the two parks.

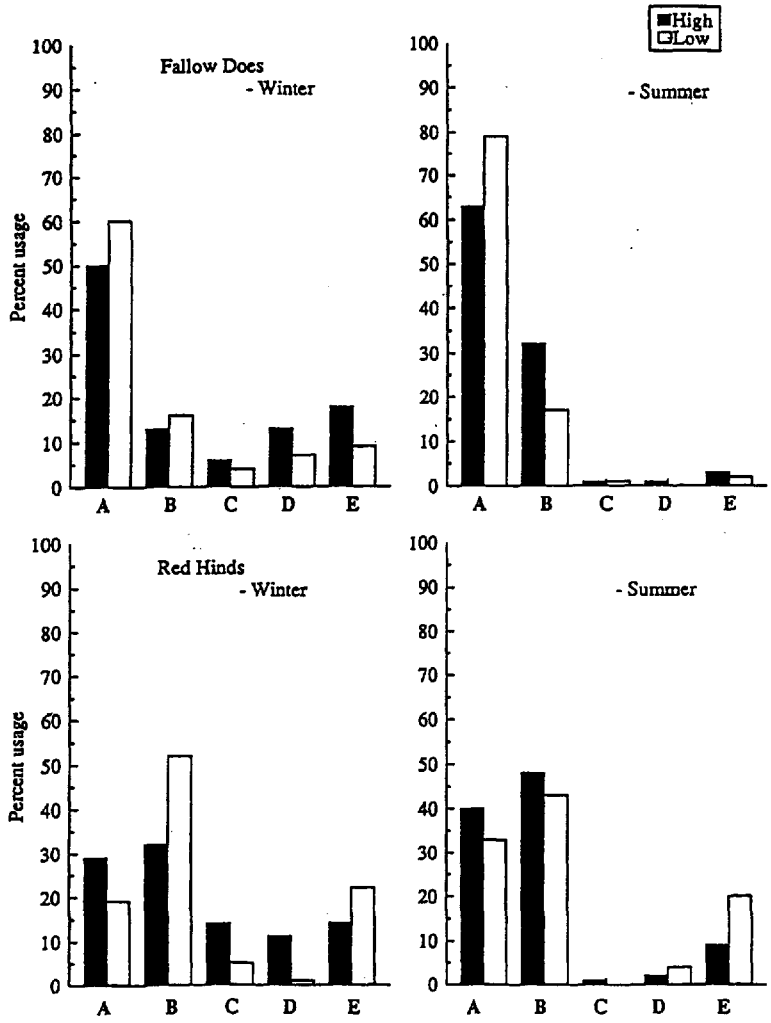

Figure 2 Patterns of habitat use by red hinds and fallow does in Richmond Park during periods of high or low levels of public usage in summer and winter. Hinds and does were selected for illustration since females of both species have been shown to display a greater response than males to any level of disturbance (Table 3). Fallow does in summer and winter show a slight decrease in the use of cover communities on days of high public access, with increased concentration of observations in open community-types; red deer hinds show decreased use of open grazing areas and open woodland, with corresponding increase in use of rough grasslands and woodland with understorey. None of the differences were however significant: $p>0.05$, see text.

Key to habitats: A: Good pastures, in the open or associated with parkland trees; B: Rough grasslands in the open or associated with parkland; C: Bracken stands; D: Woodland with no ground cover; E: Woodland with ground cover.

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Analyses were carried out separately in each site and repeated in each season for both red and fallow deer. Patterns of habitat use are illustrated in Figure 2; no significant differences in patterns of habitat use could be detected between days of high and low disturbance ($p>0.1$).

Discussion

Lavoie (1986) presents a very thorough and comprehensive review of the potential conflict of recreation and wildlife; as noted in our introduction however, remarkably little information is available on the impacts of human activity on animal populations, particularly for vertebrates. Van der Zande *et al* (1984) have published a classic series of investigations of the effects of increased human recreational activity upon bird communities in The Netherlands - demonstrating consistent effects both upon species composition and relative abundance of different species within recreational areas - with certain species actually 'encouraged' by increased human activity, others eliminated from the community. By contrast the bulk of the, admittedly limited, data which have been published for studies of large mammals suggest little or no long term effects, upon performance or behaviour (references in Introduction).

Such studies have however, for the most part been undertaken in areas where animals can move away from focal areas of human activity during periods of chronic disturbance, returning to their range after the disturbance is over; a number of more recent reports from the UK have suggested that human disturbance may have an effect on the behaviour of enclosed populations of deer in public parks, which by definition cannot so easily move away from the areas of human activity, and that such effects may have longer term implications for performance. As have these authors (Humphries *et al* 1989, Bullock *et al* in press) we have in our studies been able to show short term effects on behaviour in response to disturbance, even at the low level of people passing within 50m of the deer themselves - an event that happens sufficiently commonly one might have imagined the deer would have habituated to it totally. A greater response is elicited by deliberate approach by visitors or by dogs running off the lead. However, except in those rare instances when deer are actually harried and directly chased by dogs, the effects appear slight and we could detect no long term effect on time-budgets, patterns of habitat use, or indeed on survival (below and Putman & Langbein 1991a).

Such conclusions are somewhat at variance with those of earlier studies (eg Humphries *et al* 1989), a difference particularly striking in that their studies were also undertaken within Richmond Park; it is therefore important for us to consider reasons for this contrast of results. Work carried out by Humphries *et al* focused specifically on the fallow deer within the park, and compared group size and activity patterns of the deer between weekdays (Tuesdays) and weekends (Sundays); behaviour of the deer in Richmond was also compared with that of deer in a relatively undisturbed park nearby. Effects of disturbance on activity were assessed by considering the proportion of entire groups engaged in different behaviours in 15 minute scan surveys. Humphries *et al*

conclude that the amount of time spent feeding declined in Richmond on the more disturbed weekends, while time spent vigilant increased significantly (so that on a Sunday >80% of all animals in any group were vigilant at any one time). On the basis of 7 hours of observation during daylight hours in any one watch, they calculate a total loss of feeding time in Richmond Park of 43 minutes each weekday and 2 hours 23 minutes on Sundays.

On the basis of over 320 hours of focal animal observation, year-round, our conclusions about the effects of disturbance are more cautious. In neither Richmond nor Bushy park have the deer fully habituated even to the lowest level of possible disturbance we recorded (human passers-by within 50m) and response to other types of encounter is stronger still. However, we found such disruption of behaviour to be transitory only; animals resumed their normal behaviour very quickly after the disturbance was past. (Even after such an escalated encounter as an actual dog chase, most deer returned to their previous feeding or resting activities within 10 minutes - and often within 2-5 minutes).

We consider that Humphries *et al* over-estimated the degree of disruption to activity caused by encounters with the public through a methodology focused on the group and not the individual and through an unrealistic definition of vigilance. As noted above group-based measures markedly over-estimate the frequency with which the behaviour of any individual within the group is disrupted and equally over-estimate the length of time for which behaviour of any individual is disturbed.

That the deer do respond to disturbance is clear from the increase in frequency of vigilant groups in our data as well as theirs, (groups where >10% of animals are alert or on the move), but at an individual level reactions are less pronounced. If all disturbances are considered together, then of 42 disturbing encounters experienced by fallow bucks in Richmond or Bushy parks during our period of observation, the focal individual under observation responded only to 4 of those (or 9%); individual fallow does responded with vigilant behaviour to 11/78 disturbing encounters (14%), stags 1/46 (2%), hinds 12/77 (15.5%). Further, a return to normal behaviour was relatively rapid. Table 3 includes a summary of the proportion of groups containing >10 per cent vigilant individuals after 10 minutes of no disturbance. While we present those data as a control, to offer figures for background levels of movement or vigilance, they may also be interpreted as showing how many animals remain disturbed after a minimum period of 10 minutes after some previous disturbance. Viewed in this way it is again clear that the disruptive effects on behaviour do not persist for long. Further, analyses of time-budgets and patterns of habitat use showed no difference in our analyses between disturbed and relatively undisturbed sampling occasions.

In addition to adoption of such a group-based methodology, Humphries *et al* define vigilance in a very different way from that in which we use it here. Vigilance in their usage is defined as 'any animal whose head is raised from the feeding or sleeping position, either still or looking around, with eyes open' and thus includes 'standing head up, *head up feeding*, walking head up, running head up, *lying down head up ruminating*'.

The italics are ours and highlight behaviours embraced in such definition which are not included in that which we have adopted here.

Definitions of vigilance used by us in this report more nearly accord with those employed by Bullock and co-workers in their analyses of the effects of disturbance on behaviour of red and fallow deer in Wollaton Park (Nottingham) and Bradgate Park (Leicester) (Bullock *et al* 1990, in press). Both parks are open to the public, but the rate of encounter with potential disturbance (encounters per hour) is broadly similar in Wollaton Park in particular to that recorded at weekends in the present study. Rate of encounter with some form of disturbance was much higher among the deer of Bradgate Park, at between 20 and 30 encounters per hour. Although it is unclear from their report whether time-budgets were calculated on the basis of scan samples of groups or focal animal watches (both methods were employed) the time-budgets presented by Bullock *et al* are much more similar to those we have observed in Richmond and Bushy parks than those reported by Humphries *et al*. They suggest that, as in the present study, females (particularly red hinds) were more responsive than male deer; they further calculate that overall, the deer spend *c* 5 per cent of their time vigilant (5% fallow does, fallow bucks, red stags, Wollaton; red stags, red hinds, Bradgate. 10% vigilance, red hinds, Wollaton; <2% fallow bucks and does, Bradgate). Although encounter-rates with disturbance differed markedly between the parks, no significant difference in time spent feeding could be detected.

Long term effects of chronic disturbance upon population performance

The high potential level of disturbance to which the deer in Richmond and Bushy parks may be exposed has been a major concern to managers for some years - and it was to be one of the main objectives of our own studies that we should attempt to quantify the true level of challenge and evaluate its effects on behaviour of the deer and their performance. In order to consider what may be the long term implications of disturbance on body condition, survival and reproductive performance of the deer, we undertook a comparative analysis of differences in individual body-weights, reproductive rate and mortality across populations in 15 separate deer parks over a six year period in relation to differences in population structure/density, management or disturbance. Detailed results of such analysis are reported elsewhere (eg Langbein & Putman 1991, Putman & Langbein 1991 a, b).

In summary; high levels of overwinter mortality were found to be restricted to those populations where animals were in generally poor condition (low body-weight) at the end of cold winters and especially high in years where late-winter temperatures in January and/or February are particularly low. Low levels of mortality are experienced where stocking densities remain at or below two stock units per hectare of good grazing, where feeding of supplementary fodder overwinter commences in November rather than later in the winter and when that winter supplement provides the equivalent of 12 MJ or more ME per stock unit per day.

Public access or levels of disturbance within a park had no discernible effect upon rates of natural overwinter mortality. However, it is clear that deaths due to accident (so called 'fence-deaths' where animals suffer broken necks from running into fences, deaths due to dogs, or road traffic accidents) are significantly higher in parks with a high level of public usage ($p<0.001$). Public access thus increased the total level of mortality within a park but was **not** related to natural mortality.

Analyses of reproductive success across the same range of parks revealed a high degree of correlation between fawning success of fallow and calving success of reds within any park; clearly similar factors are influencing success in the two species. Overall, no relationship was found between fecundity of adult females and stocking densities, but levels of fecundity were higher in parks with high autumn body-weights and those where relatively high levels of supplementary feed is provided over winter. Reproductive rates were slightly, but significantly lower in those parks with a high level of public access. It would appear that this is not through an effect on conception rate or survival of calves/fawns once they are >24h old; rather we believe it is due to an increase in perinatal mortality, where mothers are disturbed immediately after parturition before they have had a chance to form a proper bond with their new offspring.

Autumn body-weights (as live-weights for fallow, dressed carcase-weights of red deer) showed a high degree of inter-correlation for all age-classes and sex-classes of deer within any one park; further, body-weights of red and fallow deer within one park were also highly correlated. Body-weights were shown to be affected by the proportion of a park's total area providing good grazing, the grazing pressure sustained by those grasslands over winter and the level of supplementary feed provided for the deer, both in that, current, and in the previous winter. Autumn/winter body-weights of both red and fallow deer also showed a significant correlation with weather, being significantly lower in wetter winters. No significant effects of public access to a park upon body-weights could be detected in multivariate analyses even after controlling for stocking rate, pasture productivity and levels of overwinter supplementation. Indeed, body-weights of both red and fallow deer at Richmond and Bushy compare favourably with the upper end of the range of weights recorded by us in general.

In brief the results of these analyses suggest that whatever may be the short term effects of disturbance on behaviour of deer in parks, overall daily time-budgets of the deer are unaffected and no consequential effects may be detected on body condition or survival within the population, although there is some evidence of a slight reduction in reproductive success due to mismothering.

Our conclusion that the response to disturbance by deer in public parks is slight should not be taken to suggest that disturbance does not matter; rather that it does not appear to have a long term effect on behaviour, nor any lasting repercussions on population dynamics of the deer population. It is clear that disturbance **does** have some effects on behaviour, affecting grouping behaviours (group sizes, cohesiveness) as shown by Humphries *et al* (1989) and temporarily disrupting feeding or periods of rest (our own data here, and again that of Humphries *et al* 1989). Further, close approach by humans

or dogs does distress the deer to a degree and dog chases not infrequently result in deaths (from the dog itself, or from consequential accidental deaths from running blindly into fences or across a busy road). Thus while we feel on ecological grounds there is little evidence to suggest that levels of disturbance within deer parks open to the public are having a significant effect on the performance of the deer herds as a whole, that is not to suggest that on purely welfare grounds some degree of control of people and their dogs in such parks might not be indicated.

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