WELFARE IMPLICATIONS OF CULLING RED DEER (*CERVUS ELAPHUS*)

E L Bradshaw[†] **and P Bateson**

Sub-Department of Animal Behaviour, University of Cambridge, Madingley CB3 0ES, UK

[†] Contact for correspondence and requests for reprints at: University of Oxford Veterinary Services, Parks Rd, Oxford OX1 3PT, UK

Final Acceptance: 15 June 1999

Abstract *Animal Welfare 2000, **9:*** 3-24

In southwestern England, red deer, Cervus elaphus, *are culled by rifle ('stalking') or by hunting with hounds ('hunting'). We compare the welfare costs of the two culling methods. Observations of hunts revealed that likely stressors such as close proximity to humans and hounds, active pursuit, noise, obstruction and physical restraint prior to despatch were very common. Other stressors, such as wounding, were rare. The blood profiles of hunted deer were compared both with injured deer, which were put down because they were thought to be suffering, and with stags stalked in the rutting season, when mature males rapidly lose weight and may be damaged in fights. Extensively hunted deer did not differ from severely injured deer in measures of muscle disruption: in hunted deer measures of red blood cell damage and psychological stress were higher. Hunted stags killed during the rut showed markedly higher levels of measures of blood and muscle cell disruption, psychological stress and fat reserve mobilization than stalked stags killed during this season. Estimates of wounding rates by stalkers showed that 11 per cent of deer required two or more shots to kill, 7 per cent took 2–15 min to die and 2 per cent escaped wounded. Overall, we judged that the welfare costs associated with hunting red deer were higher than those associated with stalking, and reducing the welfare costs associated with hunting was much less feasible than reducing those associated with stalking.*

Keywords: *animal welfare,* Cervus elaphus, *hunting, population control, red deer, stalking*

Introduction

Population control, through culling, is an integral part of red deer, *Cervus elaphus*, management in the United Kingdom. Culling is usually carried out by stalkers using high-powered rifles, but in parts of southwestern England red deer are also hunted with hounds. Whether hunting is the most humane method of culling red deer, as its practitioners claim, has been the subject of debate for many years (Williamson 1933; Anonymous 1988; Lloyd 1990; League Against Cruel Sports 1992). We have presented evidence which suggests that red deer are not well adapted by their evolutionary or individual histories to cope with the level of activity imposed on them when hunted with hounds (Bateson & Bradshaw 1997). In brief, post-mortem blood and muscle samples obtained from 64 hunted deer after death were compared with post-mortem samples from 50 non-hunted (ie stalked) red deer that had been killed with one shot to the head or neck. The effects on deer of long hunts were: depletion of carbohydrate resources for powering muscles, disruption of muscle tissue and elevated secretion of peripheral β-endorphin. High concentrations of cortisol, typically associated with physiological and psychological stress, were found. Finally, damage to red blood cells occurred early in the hunts. Nonetheless, stalking is not without its own welfare problems. Not all deer are killed outright (Green 1982) and some may escape wounded. In comparing the welfare cost of hunting with that of stalking, it is important to have some basis for an objective assessment. Otherwise, changes to culling policy designed to maximize animal welfare might have the opposite effect. In this paper, we consider both the behavioural and physiological evidence as it relates to the welfare implications of hunting red deer with hounds. We compare this evidence with the welfare issues raised by stalking.

Methods

Study areas

Field research took place primarily within the Exmoor National Park (ENP; north Devon and west Somerset) and the nearby Quantock Hills (QH; Somerset) between August 1995 and November 1996. The geography and ecology of these areas are described in Langbein and Putman (1992) and Langbein (1997).

Study animals

Hunted deer

These were wild stags and hinds hunted by either the Devon and Somerset Staghounds (DSSH), which operate over ENP, or the Quantock Staghounds (QSH), which mainly hunt the QH and surrounding area. Detailed accounts of the hunting process can be found in various historical and recent sources (eg Fortescue [1887]; Collyns [1907]; Lloyd [1975]; Whitehead [1980]; Poole [1988]; Bateson [1997]). In essence, riders use specially trained foxhounds to follow the scent of a red deer until the deer stops running and can be shot in the head from close quarters using a shotgun or pistol. 'Autumn stags' (adult males aged ≥ 5 years) are hunted between mid August and late October, hinds (adult females) between November and February, and 'spring stags' (aged between 2 and 3 years) in March and April.

Stalked deer

These were wild stags and hinds shot in the head or neck (to ensure comparability with hunted deer [Bateson & Bradshaw in preparation]) using high-velocity rifles by professional stalkers operating in Devon, Somerset and Sutherland. The stalking seasons for red deer in England cover August-April (stags) and November-February (hinds); and in Scotland the seasons run from 1 July to 20 October (stags) and 21 October to 15 February (hinds). A history of stalking is given in Whitehead (1980).

Disabled deer

These were wild red deer disabled from a variety of causes, including poor shooting, road traffic accidents, entanglement in fences, fights between stags, attacks by domestic dogs and disease. Killing them is widely considered to be the most humane option, and the deer are generally shot by hunt staff or local stalkers.

Farmed deer

These were captive-bred stags and hinds field-slaughtered for human consumption at a Somerset deer farm. Deer were shot in the head at close range with a high-velocity rifle when feeding. Witnessing the death of conspecifics did not appear to cause the deer distress (Bateson 1997; see also Anil *et al* [1997]).

Analysis of hunting activity and the behaviour of hunted deer

Distance and duration of hunts

Detailed accounts of hunts written by a hunt follower are published weekly in a local newspaper. More than one hunt may take place on each hunting day. Calculating the straight-line distances between each place name mentioned in these reports provides an estimate of the minimum distance travelled by the deer (Bateson 1997; Bateson & Bradshaw 1997). Times at which a hunt started and ended, and hence hunt duration, were calculated using both published accounts and direct observations (see below). If more accurate information was unavailable, the start time was taken as being 15min after the hunting party left the meeting place. The end time was determined by the kill or, for deer that escaped, the point at which hounds were last known to have been following the correct scent trail. For blood-sampled deer a composite standardized measure ('extent of hunt') was calculated from distance and duration measures to minimize errors (Bateson 1997; Bateson & Bradshaw 1997). Distance and/or duration measures were not obtainable for every hunt.

Habitat classification and contour analysis

Topography and habitat quality varies considerably throughout the study area (Langbein & Putman 1992; Langbein 1997), raising the possibility that sub-populations of deer differ in their physical fitness or general health. Therefore, information obtained from hunt records was also used to examine whether the location where a deer was initially found by the hunt and the topography of the subsequent hunt route (both assumed to be within the normal home range of the deer) affected hunt distance, hunt duration or blood profiles. Three habitat types were defined: i) 'moorland' (incorporating upland/coastal heaths, upland grass moor and bracken); ii) 'woodland' (broad-leaved and coniferous); and iii) 'farmland' (enclosed agro-pastoral land). The percentage area covered by each habitat type was calculated for a 1km^2 area surrounding the centrally placed start and end points of the hunt. A broad classification assigned start/end points to one of these three habitats according to which habitat had the highest percentage cover. The amounts of ascending or descending by a deer over the course of a hunt were quantified by counting the number and direction of contour lines travelled along the straight-line route estimated from the hunt record for the 1st and 3rd quartile of a hunt's extent. Two measures of the effect of the topography traversed during a hunt were then used: i) the number of contour lines crossed in ascent or descent during the first 5km; and ii) the total contour count (adjusted for hunt extent).

Direct observations and video evidence

Hunts were followed by vehicle. Behavioural observations started when the hunt began to search for their quarry and ended when a kill was made or hunting had otherwise ended. A total of 267h were spent observing hunts. *Ad libitum* recording was used to produce a detailed account of each (infrequent) sighting. The record was then broken into 15min sample intervals to obtain, on a one-zero basis (Martin & Bateson 1993), a measure of the proportion of periods in which the hunt activity was visible and, additionally, the occurrence of events considered to be potential stressors. Our direct observations were supplemented by video recordings of hunts taken by the League Against Cruel Sports (LACS) over the period of our study as part of their normal monitoring activity. Only videos where the date (and for some analyses, the time) of the recording was independently verifiable (eg by date- or timestamping) were used. In total, visual evidence was gathered on 88 hunts during 61 days of hunting by the DSSH or QSH between early August 1995 and late September 1996 (24, 12 and 25 days during the autumn stag, hind and spring stag seasons, respectively). Our direct observations provided data for 80 hunts. Video material supplemented our observational data for four hunts and provided the sole source of information for eight. Hunted deer were sighted by us at least once on 60 of the hunts we attended, with video recordings of hunted deer obtained for a further seven hunts.

Observational and video data were used to estimate the proportion of hunts where events considered to be potential stressors occurred. Potential stressors included i) coming into close proximity to the hunt. Based on our own observations and on local knowledge, we estimated deer would tolerate riders and vehicles within 50m, and pedestrians or domestic dogs within 100m before moving off. Also of interest were incidents when hunted deer ii) had escape routes obstructed by hunt members; iii) were chased by pedestrians, riders or vehicles; iv) were struck with whips; v) were handled by humans; or vi) were attacked by hounds. All these factors might contribute to poor welfare (Price *et al* 1993).

More than one type of potential stressor occurred in many hunts, and an index of the likelihood of occurrence of types (i) to (iii) was calculated as follows, using the equation:

$$(s/p - 0.5)\,(s - p/2)^2$$

where s equals the number of 15min intervals in which at least one incidence occurred and p equals the number of 15min intervals in which the hunted deer was seen. This index was designed to give more weight to cases in which a target deer had been observed in a greater number of time periods.

Observational and video data were also used to assess changes in the behaviour of hunted deer at different stages of the hunt. For each 15min interval in which we sighted the hunted deer we recorded details of its gait. The five categories used (lie, stand, walk, trot and run – ie canter or gallop) were not mutually exclusive, since each might be seen in one 15min interval and each received a score of 1 if seen to occur at least once during that time. Thirty min time periods were used during analysis in order to increase sample sizes in the longer time periods. Only one observation from each animal was used for each time period, with a mean score obtained for multiple sightings. We also scored the ability of a deer to jump obstacles such as fences and hedges. Deer were categorized as 'tired' or 'not tired' based on a subjective impression of their physical state (Bateson 1997). Hunt members use such impressions when assessing whether the deer in view is the hunted animal or not. Analyses for behavioural measures other than gait measures were based on 1h time periods.

While observations of hunted deer took precedence, data on the behaviour of 'non-hunted' deer (those seen during the course of a hunt but not the intended quarry) were also collected whenever possible. Non-hunted deer (individuals or groups) were seen on 123 separate occasions on 38 different hunts. Sightings of groups were treated in the same way as sightings of individuals if all group members were behaving similarly.

Wounding rates associated with stalking

Four methods were used to obtain estimates of the frequency with which stalkers wounded deer, and the proportion of deer that escaped wounded.

i) Retrospective records were obtained by asking eight stalkers (three accompanied amateurs and five professionals) to recall numbers of deer shot and wounded over the previous season.

ii) Seven stalkers not involved in the retrospective analysis kept detailed records throughout the 1995–1996 stalking season of when and how every deer was shot, and the subsequent fate of each animal. All seven were experienced marksmen.

iii) We wrote to more than 130 game dealers requesting that, for each red deer they received, they would indicate on a diagram of a dressed carcase (ie carcase minus the head, viscera and feet) where in the body it had been shot and whether or not the carcase showed signs of old injuries. Of the minority of game dealers who handled red deer, six agreed to help and filled in left and right side profiles of red deer carcases indicating the rifle bullet wounds on the visible carcase. The dealers were also asked to mark the positions of old wounds and whether they were from shotgun pellets or rifle bullets. We received 40 replies. These had the details of the game dealer removed, were copied and sent independently to seven expert stalkers, one of whom had participated in the retrospective study, and six who had kept current records. These stalkers were asked to estimate how far each deer probably ran after the shot indicated on the diagram and whether it might have required a second shot.

iv) Hunt staff and local stalkers may be called out on occasion to kill wild deer that are badly injured or diseased. We examined the records describing the physically injured animals to determine what proportion of these casualties might have resulted from poor shooting.

Another approach, based on the likelihood of wounded animals being found, was used to obtain information on probable wounding rates. We took a highly conservative figure of 2500 for the population of red deer (including overwintered calves) in the study areas (see Langbein & Putman [1992]). To maintain a stable population would require 20 per cent of the total to die every year as a result of culling and other causes (Clutton-Brock & Lonergan 1994; Langbein & Putman 1996). We assumed that 15 per cent of the total population were culled by stalkers, and estimated the total number that would have escaped wounded for different rates of wounding. We then examined the nature of injuries in the disabled group of deer from ENP and the QH, using both our own records and records from previous years kept by the hunts.

Age, body condition and blood profiles of hunted, rutting and injured deer

Comparisons between deer killed by hunters and stalkers during the rut

The peak rutting season was defined as 24 September to 24 October, the period where most interactions and displays between harem-holding stags take place (Clutton-Brock *et al* 1982). Adult hinds killed by stalkers between November and January were used as a comparison group because few mature stags were sampled by stalkers outside of the peak rutting season. Age was determined from lower jawbones using tooth eruption as the main criterion (Mitchell 1967; Ratcliffe 1987). Data for hunted stags killed during the rut in the study year were limited, and so were combined with data on hunted stags obtained by J Langbein during the 1994 rutting season (J Langbein personal communication 1997).

Many of the stalked deer came from Sutherland, which has poorer quality habitat for red deer than southwestern England. The average weight of adult deer sampled from Sutherland was much lower than that for adults from the study area in England (Bateson & Bradshaw in preparation); these findings correspond with those of more extensive studies (Langbein 1997). We obtained estimates of physical condition from one or both of two indices of abdominal fat reserves: a kidney fat index (KFI; the weight of the fat surrounding the kidney as a percentage of the total kidney weight); and an estimate of the percentage of kidney covered by fat (KF %) (Riney 1982). As KF % values were obtained more often than KFI

ones, KFI values were converted to the former using the following regression equation, derived from the 19 sampled deer where both measures were obtained:
$KF\ \% = 16.1 + 1.23KFI$.

Physiological comparisons between hunted, stalked and injured deer
Injured deer comprised both double-shot stalked deer and disabled categories. Deer that were double-shot by stalkers had been wounded by the first shot (invariably a body shot) and killed by the second; time from first shot to death was, according to the stalkers, less than 15min. Disabled deer were arranged in subgroups according to the type and duration of their injury. Hence, deer with limbs broken at or below the elbow, classified as 'limb' injuries, were compared to those with more extensive injuries to muscle mass, internal organs or bone (including shoulder, pelvic or upper limb injuries), classed as 'body' injuries. Deer with 'recent' injuries (estimated to be no more than 1 week old) were compared to deer with 'old' injuries (partially or totally healed). Comparisons were made between the double-shot deer and disabled subgroups to check for homogeneity.

Blood sample collection
Blood samples from all farmed deer and a few stalked deer were collected post-mortem by one of the authors; the majority of other deer (including disabled animals) were sampled by the stalker or hunt personnel responsible for the kill. Ideally, collection tubes were filled with free-flowing blood when deer were being bled out (Bateson & Bradshaw 1997). Providing that blood is collected from deer shot in the head or upper neck, the site where blood is obtained has little effect on most blood measures (Bateson & Bradshaw in preparation). Hence, blood samples taken from the heart and chest cavity of the hunted and stalked deer were included in the analyses.

Blood assays
Whole blood samples were centrifuged to separate out the plasma fraction (Bateson & Bradshaw 1997). Then, assays for alanine amino transferase (ALT), alkaline phosphatase (ALP), gamma glutamyl transferase (GGT), glutamate dehydrogenase (GLDH) and concentrations of urea and total protein were performed at 37°C by the University of Bristol's Department of Clinical Veterinary Science (Division of Companion Animals, Langford) using a Kone Supra Discrete auto-analyser (Kone Instruments, Espoo, Finland). Concentrations of β-hydroxybutyrate (β-HB), haemoglobin, myoglobin and total calcium were assayed by the Department of Clinical Biochemistry at Addenbrooke's Hospital, Cambridge using enzyme-linked reactions in conjunction with a centrifugal analyser (for β-HB); electrophoretic techniques using agarose gel on a Gelband (FMC Bioproducts, Rockland, USA) plastic backing sheet (for haemoglobin and myoglobin; Fairbanks 1976); and a photometric method based on a modification of the calcium-*o*-cresolphthalein complexone reaction, using DADE reagents and the DADE Dimension™ XL analyser (Dade Behring Ltd, Milton Keynes, UK) for total calcium (Endes & Rude 1994). An index of plasma colour was obtained by matching samples by eye to a range of colours generated by Adobe Photoshop™ 2.0 (Adobe Systems Inc, California, USA), using the yellow (Y) and magenta (M) components of the CMYK process colours (Bateson 1997). Details of assay techniques and laboratories used for 13 other measures, namely, levels of acidity (pH), activities of aspartate amino transferase (AST) and creatine kinase (CK), and concentrations of β-endorphin, total bilirubin, chloride, creatinine, cortisol, free fatty acids (FFA), haem (the

pigment portion of the haemoglobin and myoglobin molecule), lactate, potassium and sodium are given in Bateson and Bradshaw (1997).

Inter-assay coefficients of variation (CV) were < 5 per cent for all variables except ALP (5.3%), low levels of β-endorphin, total bilirubin (17.5%), CK (11.5%), high levels of cortisol (6.6%), GGT (13.7%), GLDH (12.7%), low levels of lactate (6.3%) and LDH (7.52%). Intra-assay CVs were < 3% for all measures except low levels of β-endorphin (9.6%), high levels of cortisol (7.6%), GGT (6.4%) and GLDH (9.4%). Where possible, we obtained details of circumstances that might affect the profiles (eg the distance covered by a hunted deer, how far a stalked deer ran after being shot, the nature of a disabled deer's injury).

Blood sample lability

Collection of samples in the field meant that it was impossible for us to standardize the time from death to centrifugation of the blood (median time 4.06h, inter-quartile range 2.88–5.69 h), and storage temperature during this period was not always consistent. In order to provide some guidance as to the lability of the measures, a study was conducted on a total of 24 field-slaughtered farmed deer, in which time from blood collection to centrifugation was varied. Centrifugation times (24, 54, 119, 263, 585, 1299 and 2880 min after collection) were chosen so that intervals between them were the same on the logarithmic scale and a 48h period was covered. Time elapsing between death and sample collection varied between 1 and 10 min (mean 5.5min).

To facilitate the collection of multiple samples and to reduce the incidence of clotting, blood from each deer was collected into a clean plastic jug during exsanguination, before transfer to 13 separate 10ml tubes containing lithium heparin. Tubes were kept at ambient temperature until the first could be spun down (after 24 or 54 min); thereafter, half the remaining samples were stored at 4°C and half at room temperature until centrifugation.

Regression tests for the effects of time lapse and storage temperature on the stability of blood variables were carried out for all measures except concentrations of glucose and haem. Sample sizes varied as sufficient plasma was not always available to conduct every assay for every time period sample for every deer. Regression lines were fitted to each measure from each individual, analysing the data separately for chilled and room temperature samples. Mean values were obtained for the gradients of the changes over time. Matched, paired *t*-tests were used to assess the statistical significance of the departure of mean observed gradients from a zero gradient. Observed gradients for most measures showed no significant departure from zero ($P > 0.05$; Bateson & Bradshaw unpublished data). However, four measures were markedly affected by the time between blood collection and centrifugation and/or storage temperature (namely, sodium, potassium, lactate and FFA) and one, LDH, marginally so (Table 1). Data for these measures for individual deer were corrected according to the following formula:

$c = o - mt$

where c = corrected value, o = observed value, m = gradient obtained from the time-course study of farm deer (taking the chilled or room-temperature gradient as appropriate) and t = time from collection to centrifugation.

Statistical analyses

Statistical analyses were carried out using Minitab® Release 10.51 Xtra software (Minitab Inc, State College, USA). Analysis of variance (ANOVA), using a general linear model technique, was used for most statistical analyses or, where appropriate, *t*-tests. Assumptions of normality and homogeneity of variance were checked. When looking at blood measures, the distribution of residuals was examined for each blood analyte for each red deer group. Where the residuals were random, results are presented as means ± standard deviation (SD). For non-random residuals, data were transformed to normal by taking natural logarithms and are presented as medians with inter-quartile ranges (IQR). All tests were two-tailed.

Table 1 Significant rates of change of plasma assay levels when time and temperature of collection and centrifugation of whole blood were varied. $^*P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$.

Variable	Unit	Chilled			Room temperature		
		Mean[2]	SD	t^1	Mean	SD	t^1
FFA	μmol l^{-1} h^{-1}	0.41	0.51	2.78*	0.97	0.41	8.28***
Lactate	mmol l^{-1} h^{-1}	0.01	0.04	1.27	0.05	0.03	6.21***
LDH	iu l^{-1} h^{-1}	-0.70	3.34	-0.73	8.39	10.08	2.89*
Potassium	mmol l^{-1} h^{-1}	0.24	0.15	5.67***	0.10	0.12	3.01*
Sodium	mmol l^{-1} h^{-1}	-0.21	0.21	-3.39**	0.12	0.28	1.45

FFA – free fatty acids; *LDH* – lactate dehydrogenase.

[1] The *t* values are from a matched, paired *t*-test between the observed gradient and a gradient of zero: signs show direction of deviation from 0; *df* = 10.

[2] The mean gradients reported in Table 1 were initially reported in Bateson & Bradshaw (1997).

Results

Analysis of hunting activity and the behaviour of deer

Distance and duration of hunts

Of the 170 DSSH and QSH hunts analysed over the 1995–1996 and partial 1996–1997 seasons, 79 ended in a kill. Irrespective of the sex of the deer, hunts ending in a kill were significantly (mean ± SD) longer than hunts where the deer escaped (19.4 ± 1.3 km, n = 79 and 15.0 ± 1.2 km, n = 88 respectively; $F_{1,165} = 5.91$, $P \leq 0.05$). (Three hunts were excluded from the distance analysis because a reliable estimate of hunt distance was not possible.) Nonetheless, in hunts that ended with the deer escaping, the majority (98%) were longer than 5km (the distance of the shortest hunt leading to a kill), 78 per cent were longer than 10km, and 25 per cent were longer than the average length of hunts ending in a kill. Hind hunts tended to be shorter in duration than either autumn or spring stag hunts (2.4 ± 0.3 h, n = 27 for hinds and 3.3 ± 0.15 h, n = 85 for all stags; $F_{1,110} = 9.66$, $P \leq 0.01$), irrespective of how the hunt ended.

Straight-line distances between the start and end points of hunts ending in a kill were much shorter than the total (mean ± SD) distance covered by these hunts (5.2 ± 0.4 km and 19.1 ± 7.4 km, respectively; $t_{83} = 13.90$, $P \leq 0.001$), suggesting that deer tended to back-track and circle during a hunt. Straight-line start-to-end distances were not related to season ($F_{2,58}$ = 1.55).

Habitat classification and contour analysis

For hunts where deer were killed, we found that the starting habitat did not predict the subsequent length of a hunt. We repeated the analysis leaving autumn stags out, since the area in which they rut (and are hunted) may not be the same as that where they spend the majority of the year, but this had no effect. End habitat was associated with hunt distance ($F_{2,58}$ = 6.33, $P \leq 0.01$); this was not a seasonal effect. Here, hunts ending with a kill in 'woodland' had a shorter (mean ± SD) distance (14.69 ± 1.4 km, n = 16) than those ending in 'farmland' (19.33 ± 0.98 km, n = 33), which were shorter than those ending on 'moorland' (25.41 ± 1.63, n = 12). Neither start nor end habitats, however, were associated with hunt duration or straight-line distances between the start and end points. Overall, 55 per cent to 60 per cent of DSSH hunts ended with the deer in or near streams, rivers or other bodies of water. Running to water was rarer in the QSH hunts, probably because there are fewer major watercourses in this area.

The number of contour lines over which a deer ascended or descended during the first 5km of a hunt did not predict the length of a hunt when ascents/descents were considered separately, nor when they were added together. Nor was there any difference in the contour to distance ratio between the 1st and 3rd quartile of hunt extent.

Behavioural observations

Close encounters between hunted deer and hunt members or hounds were common (Table 2). Of the 67 hunts where hunted deer were seen or videotaped, the hunted deer came within 100m of pedestrians or hounds at least once on 47.8 per cent and 32.9 per cent of hunts, respectively; and within 50m of riders or vehicles on 22.4 per cent and 19.4 per cent of hunts, respectively. Not surprisingly, hounds in close proximity to hunted deer were nearly always pursuing them (Table 2). 'Pursuit' by riders (intentional or otherwise) was also common (Table 2). The frequency with which hunt members came into close contact with the hunted deer was reflected in the proportion of hunts (26.9%) where the path of a hunted deer was either accidentally or deliberately obstructed. Deliberate attempts to obstruct the path of a hunted deer occurred in 25.4 per cent of all hunts seen and involved shouting, sounding car horns and driving, riding or running towards the animal or towards its escape route.

Table 2 Close encounters between hunt members or hounds and hunted deer and instances of 'pursuit', expressed as a percentage of the 67 hunts in which deer were seen or videotaped, regardless of the ultimate fate of the deer.

Event	Hunt members			Hounds
	On horseback	In vehicles	On foot	
Proximity 0–10 m	6.0%	4.5%	10.5%	11.9%
> 10–50 m	16.4%	14.9%	19.4%	10.5%
> 50–100 m	-	-	17.9%	10.5%
Pursuit	19.4%	3.0%	4.5%	32.8%

Dividing hunts into 15min intervals, most hunts had a mean (and range) of 12.21 (3–32) intervals, with the hunted deer sighted during 1.58 (0–7) of these. Although it has been suggested that deer mainly come into close contact with hunt members or hounds at the beginning and end of a hunt, we found (chi-square test on sightings made in first, middle and final half hour) that sightings of hunted deer were randomly distributed (chi-square = 1.85, *df* = 2, ns); as was the incidence of potential stressors (chi-square = 5.90, *df* = 2, ns). The combined effects of proximity, pursuit, noise and obstruction were assessed using an index of their likelihood of occurrence. The higher this index, the shorter the hunts ($F_{1,17} = 7.27$, $P < 0.05$).

Video evidence purporting to show hunt followers striking deer with whips was not convincing. We did not observe such incidents ourselves. No evidence was made available to support claims that calves are whipped to separate them from hinds during the hind-hunting season. We did not ourselves see any incidents of hounds biting deer, despite one-third of all 15min observation periods containing sightings of hounds. However, we studied carefully the videotapes where it was alleged that the hunted deer was attacked by hounds, and were convinced by this evidence on one occasion (QSH; 29 August 1995). This represents only 3.4 per cent of the hunts leading to a kill where the hunted deer was sighted, but 25 per cent of all kills for which we have visual evidence.

Two of the four deer that we witnessed or were videotaped being killed by the hunt were not killed instantly with the first shot (Bateson 1997), representing 6.3 per cent of the hunts leading to a kill where the hunted deer was sighted, but 50 per cent of all kills for which we have visual evidence. The physical restraint of deer by humans was seen on three of the hunts leading to a kill (10.3% of the total). Handling by humans, like biting by hounds, is most likely to occur just before a kill, and the close proximity of people around the deer would mean that a pistol rather than shotgun was used to despatch it. The DSSH Masters estimate they use a pistol about twice a month in the hunting season, and the QSH Master about 6 times in the total hunting year. This corresponds to an estimated 20–30 per cent of all kills (although not all of these will necessarily involve much handling since pistols are also used to dispatch deer that are not killed outright by shotgun).

Running was by far the most common pace of a hunted deer, recorded on 85 per cent of the occasions when hunted deer were seen. Trotting was seen 20 per cent of the time, but lying down, standing and walking were relatively uncommon (recorded on 10%, 13% and 4% of sightings, respectively). Deer were more likely to be seen lying down, standing or walking as a hunt progressed ($F_{6,96} = 2.31$, $P \leq 0.05$; $F_{6,96} = 2.84$, $P \leq 0.05$; and $F_{6,96} = 4.26$, $P \leq 0.001$, respectively), but sightings of trotting and running did not vary with stage of hunt ($F_{6,96}$=1.88; $F_{6,96} = 0.37$, respectively). Deer were significantly more likely to be scored as 'tired' after the first hour ($F_{2,54} = 6.57$, $P \leq 0.01$).

The behaviour of non-hunted deer seen near a hunt

Table 3 summarizes the behaviour of non-hunted deer seen near a hunt. The great majority were judged to show some sign of disturbance. On almost half of these occasions deer were being actively chased by hounds or, less frequently, pursued solely by members of the hunt. Even when chasing was not observed, the deer tended to move away from the area where the stag hounds were operating, usually at a run (84.8% of sightings) or, less often, a trot (15.2%). Most of the deer were still moving away at a run or trot when we lost sight of them. However, some slowed to a walk or stopped, and a few returned to the general area that they had been seen leaving. Deer rarely remained near a hunt or hunting activity. Of nine such occasions, three involved deer milling around in a restless fashion after riders and hounds (not hunting at the time) had passed nearby. On six occasions deer were observed standing still but very alert, clearly watching nearby hunting activity. Hounds were seen passing within 200–300 m of the deer on four of these occasions, on three occasions actively hunting and on one occasion being escorted by hunt staff to another area. Behaviours that we considered to indicate overt signs of panic (such as falling, running into objects or misjudging jumps) were only seen on three occasions (2.5% of all sighting of disturbed deer) but on no occasion resulted in obvious injury. On very few occasions did non-hunted deer show no obvious behavioural signs of disturbance.

Table 3 Behaviour of non-hunted deer seen near a hunt.

Reaction	Proportion of sightings	Percentage
Disturbed	**118/123**	**95.9**
- Chased	57/118	48.3
- Not chased	61/118	51.7
(i) Move away:	52/118	44.1
- Leave area	43/52	82.7
- Stop	7/52	13.5
- Return	2/52	3.8
(ii) Remain	9/118	7.6
Not disturbed	**5/123**	**4.1**

Wounding rates associated with stalking

Retrospective records showed that, of 372 red deer killed by eight stalkers, a mean (± SD) of 7.5 ± 1.7 per cent had survived more than 2min after the first shot, 12.0 ± 3.0 per cent were killed using two or more shots and 3.5 ± 1.5 per cent escaped wounded. Records kept over the 1995–1996 season (see, *Methods*) showed that, of 171 red deer killed by seven other stalkers, means (± SD) of 4.4 ± 2.3 per cent had survived more than 2min after the first shot, while 9.8 ± 3.0 required two or more shots to kill and none were recorded as having escaped wounded. The (mean ± SD) distance run by these deer when shot in the chest (n = 44) was 31.9 ± 0.6 m, whereas deer shot in the head or neck (n = 45) ran 3.2 ± 0.5 m. Of the 40 deer represented in the carcase diagrams returned from the game dealers, two (5%) had old wounds from shotgun pellets, 14.6 ± 3.3 per cent were estimated to have survived for more than 2min after the first shot and 10.0 ± 2.8 to have required two or more shots to kill. The three methods give remarkably consistent results.

Weighting the averages of the proportions of animals requiring two or more shots to kill (obtained from the various different measures) by the number of animals involved, gives an overall average of 11 per cent. Similarly, the overall average for the proportion that took more than 2min to die is 7 per cent. These two groups do not overlap entirely. For example, sometimes deer fatally injured with a single, well-placed body shot may take more than 2min to die (although no deer in our sample took more than 15min), but an animal wounded by the first shot may be killed by a second or third within the space of 2min. The overall average for the proportion of animals that were wounded but not recovered was 2 per cent.

A wounding rate of 2 per cent would have resulted in an estimated eight deer escaping wounded per year over the whole of ENP and the QH (based on a population size of 2500, with 15 per cent culled by stalkers). Wounding rates of 15 to 45 per cent, reported elsewhere (Staines 1985; E Marriage personal communication 1997), would have resulted in between 56 and 169 injured deer escaping per year. Of the 23 deer in the disabled category for which we received a reasonable description of their condition, three had rifle wounds and one had a shotgun wound. We examined the DSSH's own records of the injured, diseased or dead red deer they had dealt with in the 1994–1995 and 1995–1996 hunting seasons. The total numbers were 32 and 56, respectively, excluding the remains of animals killed by poachers. Of these, 9 (1994–1995) and between 4 and 8 deer (1995–1996) appeared to be casualties of poor shooting. While some animals undoubtedly die without being found, these figures nonetheless correspond remarkably well with estimates of rifle wounds obtained by our other techniques.

Age, body condition and blood profiles of hunted, rutting and injured deer

Hunting

In addition to the results described in Bateson and Bradshaw (1997), we found that the straight-line distance between the start and end points of hunts accounted for some of the variation in β-endorphin concentrations; regression showed that larger distances were associated with higher levels of the hormone (r^2 = 15.5% when adjusted for effect of overall hunt distance; $F_{1,50} = 6.28$, $P \leq 0.01$). The relationship with cortisol concentration was not significant, probably because cortisol rapidly reaches a ceiling (Goddard *et al* 1994).

Comparison between hunted and stalked stags killed during the rutting season

Stalked stags did not differ in age from hunted stags, but were older than hinds (means ± SD: 5.8 ± 1.1, 5.8 ± 1.8 and 4.6 ± 1.6, respectively; $F_{2,38} = 5.99$, $P \leq 0.01$). Indices of body condition in hunted deer did not differ from English stalked deer even when the time of year was entered as a covariate ($F_{1,98} = 1.4$). However, the Scottish deer had a significantly smaller covering of kidney fat (KF %) than the English deer when the time of year was entered as a covariate ($F_{1,98} = 9.45$, $P \leq 0.01$). That no statistically significant difference was found between hunted and stalked stags killed during the rut ($F_{1,8} = 1.1$, ns) may reflect the small sample sizes involved. In all animals, KF % declined from autumn to spring ($F_{1,99} = 27.89$, $P \leq 0.001$).

Stalked stags killed during the rut differed from stalked hinds in only five plasma measures: levels of acidity ($F_{1,36} = 7.88$, $P \leq 0.001$), and concentrations of haem ($F_{1,34} = 4.7$, $P \leq 0.05$), bilirubin ($F_{1,34} = 6.5$, $P \leq 0.05$), creatinine ($F_{1,35} = 22.4$, $P \leq 0.001$) and FFA ($F_{1,31} = 32.8$, $P \leq 0.001$). The (mean ± SD) level of acidity for hinds was pH 8.02 ± 0.03. Medians and IQR for hinds for the other measures were, respectively, 3.0 (1.4–4.0) μmol l^{-1}, 4.8 (4.4–5.5) μmol l^{-1}, 115 (107.0–120.5) μmol l^{-1} and 59.4 (34.3–89.0) μmol l^{-1}.

There was no statistically significant difference between hunted and stalked stags in some plasma measures, namely, concentrations of urea, protein, chloride, ALT, GGT, GLDH and potassium (Bateson & Bradshaw unpublished data) and β-endorphin (Table 4). Differences in ALP were not clinically important (see Alexander & Buxton [1994]). However, of interest were the significantly lower plasma acidity and higher blood haemolysis of rutting stags killed by the hunts compared with those stags killed by stalkers, as well as the higher plasma concentrations of cortisol, FFA and activities of enzymes associated with muscle disruption (Table 4).

Comparison between hunted and injured deer

Hunted deer are compared with all injured deer (ie containing the double-shot and disabled groups) in Table 5. The hunted deer had significantly higher plasma concentrations of cortisol and β-endorphin than the injured deer. Their plasma was significantly more deeply coloured on both the magenta and yellow scales and the FFA levels were significantly higher. They also had significantly higher levels of urea, protein, albumin, creatinine and sodium, as would be expected from the well-known effects of exercise on blood concentration (Hoppeler & Billeter 1991). They did not differ from the injured deer in the activities of muscle-derived enzymes (AST, CK and LDH) in the plasma. Entering time of year as a covariate did not affect any of the differences.

Table 4 Contrasts between plasma constituents (various measures, as shown) for shot or hunted stags during the rutting season. *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

Analyte	Unit	Hunted			Stalked			
		n	Mean (median)	SD (IQR)	n	Mean (median)	SD (IQR)	*F*
Acidity	pH	14	7.82	0.21	8	8.21	0.25	15.43***
ALP[1]	iu l^{-1}	12	(38.5)	(27.5–79.5)	8	(97.0)	(63.7–300.0)	8.2**
AST[1]	iu l^{-1}	12	(156.5)	(140.2–214.0)	8	(81.0)	(51.2–97.0)	25.8***
β-End	pmol l^{-1}	15	252.9	174.2	9	162.6	79.5	2.1
Bilir[1]	µmol l^{-1}	12	(21.7)	(13.4–32.1)	8	(6.1)	(5.4–7.4)	31.27***
CK[1]	iu l^{-1}	12	(3170)	(1060–3788)	8	(265.5)	(221.3–386.7)	46.5***
Creat[1]	µmol l^{-1}	12	(266.0)	(217.7–315.5)	8	(146.5)	(125.8–173.5)	40.1***
Cort[1]	nmol l^{-1}	16	(202.5)	(157.0–236.8)	9	>2.7	(2.7–20.8)	137.1***
FFA[1,2]	µmol l^{-1}	8	(911)	(502–1374)	7	(299)	(117–499)	6.99*
Haem[1]	µmol l^{-1}	12	(32.0)	(26.0–108.6)	8	(4.1)	(3.0–8.8)	28.77***
LDH[1,2]	iu l^{-1}	12	(1417)	(1039–1718)	8	(826)	(672–946)	15.9***
Na[1,2]	mmol l^{-1}	12	145.5	6.39	8	138.8	6.84	4.9*

ALP – alkaline phosphatase, *AST* – aspartate aminotransferase, *β-End* – β-endorphin, *Bilir* – bilirubin, *CK* – creatine kinase, *Creat* – creatinine, *Cort* – cortisol, *FFA* – free fatty acids, *Haem* – haemaglobin, *LDH* – lactate dehydrogenase, *Na* – sodium.

[1] General linear model applied to log-transformed data.

[2] Correction applied for time between collection and centrifugation of blood sample to account for lability of measure.

The injured group was heterogeneous, including animals with injuries to different parts of the body and injuries inflicted at different times before they were killed and blood samples obtained. The hunted group was also heterogenous in the sense that the deer had been hunted for different distances and lengths of time. Animals in the disabled group which were judged to have the worst injuries (see, *Methods*) were compared with hunted animals that had been hunted to the greatest extent (the top quartile). Although the values of the critical variables were higher in both groups, as would be expected, the direction of the differences between the groups was the same as shown in Table 5 except that plasma AST activity was significantly higher in the injured animals ($F_{1,21} = 5.93$, $P \leq 0.05$).

When injured animals were split into three subgroups according to the recency of their injuries (those killed ≤ 15min after their first injury, those injured 1–3 days before death and those with older injuries) three significant non-linear effects were found in AST, CK and ALT activity ($F_{1,20}$ = 5.11, $P \leq 0.05$; $F_{1,20}$ = 5.65, $P \leq 0.05$; and $F_{1,20}$ = 4.52, $P \leq 0.05$, respectively). In each case, the increase was significant in the first few days after injury and the subsequent decline was not. No other measure was affected by the recentness of the injury.

Table 5 Contrasts between plasma constituents (various measures, as shown) for hunted deer *vs* injured deer (combined 'disabled' and 'double-shot' groups). See Table 4 for definitions of abbreviations and units of analytes. *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

Analyte	Hunted			Injured			*F*
	n	Mean (median)	SD (IQR)	n	Mean (median)	SD (IQR)	
Albumin	53	36.6	6.4	33	32.1	7.95	8.19**
ALT[1]	44	(47.0)	(41.25–60.75)	33	(52)	(34–82)	2.18
AST[1]	54	(177)	(131–291)	33	(153)	(90–506)	1.31
CK[1]	54	(3459)	(1791–5921)	33	(1578)	(500–8792)	2.31
ColM	50	51.74	22.62	34	31.2	29.3	13.05***
ColY[1]	50	(93.5)	(86–100)	34	73.1	21.5	22.51**
Cort	60	(197)	(161–236)	33	(120.0)	(13.1–200.5)	30.46***
Creat[1]	53	(167)	(131–207)	33	(118)	(90–148)	33.08***
β-End	58	280.8	168.3	36	195.9	144.0	6.30*
FFA[1,2]	43	(833)	(460–1168)	23	(240.6)	(94.2–392.1)	28.74***
LDH[1,2]	53	(1732)	(1187–2537)	33	(1229)	(793–1973)	3.08
Protein	53	66.5	13.4	33	60.0	14.7	4.40*
Na[2]	53	145.8	5.2	32	142.2	5.7	7.99*
Urea	53	9.1	3.9	33	7.3	4.0	4.37*

ALT – alanine aminotransferase (iu l^{-1}), *ColM* – magenta component of plasma colour (%), *ColY* – yellow component of plasma colour (%). Units for albumin and protein are g l^{-1}, and mmol l^{-1} for urea.

[1] General linear model applied to log-transformed data.

[2] Correction applied for time between collection and centrifugation of blood sample to account for lability of measure.

Discussion

The welfare consequences of hunting

Evidence from behavioural observations

The view that deer will pay no heed to hunting activity unless they are the quarry (Lloyd 1990) does not seem well founded. Even on the infrequent occasions where deer stood and watched a nearby hunt it would be unwise to assume the animals were unaffected. First, internal reactions to a stressor, such as elevated heart rate, may not be accompanied by a visible change in behaviour (MacArthur *et al* 1979). Second, running from predators consumes both energy and time that could be spent on other activities, such as feeding. Learning to assess risk accurately has great survival value (see Lingle [1998]). Predation risk is not constant and deer, like any prey species, are likely to respond in different ways under different circumstances to the appearance of a predator (Estes 1991; Sapolsky 1994).

Does disturbance from hunting give cause for concern from a welfare viewpoint? Although most deer were seen leaving the immediate vicinity of the hunt, overt signs of panic were rare. Radio-telemetry studies show that deer in hunted areas have small, stable home ranges (Langbein & Putman 1992; Langbein 1997), so deer clearly do not move great distances for any length of time. Two hinds fitted with radio-transmitters did not leave their home range areas when hunting took place there, although they travelled twice as far on that day than on days when there was no hunting (Bateson 1997). This greater activity might be costly at times of year when body reserves are low and food quality is poor. However, the consistently high bodyweights, good condition and fecundity of deer in the study area (Langbein 1997) do not suggest that disturbance from hunting is detrimental in this respect.

While hunting may not adversely affect the welfare of non-target deer, the same is unlikely to be true for deer that are actively hunted. The physiological consequences of the chase itself are severe (Bateson & Bradshaw 1997), despite the varied pace of a hunt allowing deer to slow or stop periodically. Behavioural data indicate that even tiring animals continued to exert themselves maximally throughout the hunt whenever threatened by hounds or humans. The likelihood of observing cantering or galloping within a 15min observation period did not vary with the length of the hunt, yet the likelihood of observing slower gaits and a subjective estimate of fatigue increased significantly as the hunt progressed.

Many of the public's concerns about the effect of hunting on the welfare of red deer relate to the perceived behaviour of members of the hunt. The likelihood of some events happening, such as striking at calves and hinds with whips in order to separate them, or goading on deer that are reluctant to run, have probably been exaggerated by the opponents of hunting. Other events, such as deer being attacked by hounds, or being wounded rather than killed instantaneously when shot at the end of a hunt, definitely do occur, but we cannot say with what frequency. (It should be pointed out that wounded deer are probably subsequently killed relatively quickly. Also, that the chances of deer escaping wounded must be very low indeed, providing the hounds are on hand to follow them up.) Handling deer prior to killing them occurs in many hunts. It is liable to cause the animals considerable distress and may present an appreciable welfare problem.

Less dramatic but far more frequent events, such as hunted deer coming into close proximity to members of a hunt or the hounds, or having their escape route obstructed, had a quantifiable effect on the deer. For hunts that ended in a kill, the length of the hunt was inversely related to the frequency with which these events occurred. Although cause and effect cannot be proven, a reasonable explanation of this result is that frequent contact with humans or hounds may cause a deer to exert itself more (ie by repeatedly trying to distance itself from the threat) and hence tire more quickly. The noise from shouting, car horns, etc that accompanies deliberate attempts to obstruct the path of a deer may, in itself, be a significant source of stress (see Price *et al* [1993]). Deer that are prevented from following a known escape route may be chased into unfamiliar countryside and become disorientated. Hunted deer are known to run through villages, gardens or even into buildings. The adverse effects for these animals are likely to be considerable. Therefore, human presence is likely to add significantly and adversely to the welfare implications of hunting with hounds.

Evidence from blood profiles of rutting deer

The physiological changes experienced by a hunted deer might not differ substantially from those experienced as part of the normal life history of this species. For example, stags are clearly under considerable physiological stress during the rut. At this stage of their reproductive cycle they have high energy costs and reduced food intake, and may lose as much as 20 per cent of their bodyweight (Clutton-Brock *et al* 1982). They are also subject to frequent aggressive encounters with other males, and are at risk of injury (Clutton-Brock *et al* 1982). Arguably, the fewer the differences between the physiological profiles of stalked and hunted stags killed in the rut, the less justification there is for believing that the pronounced physiological changes found in hunted deer indicate a welfare problem.

Comparing stalked stags with stalked hinds gave some indication of the effect of the rut on plasma measures. Stags fast during the rut and must draw on their fat reserves – this accounts for higher FFA levels in stags than hinds. The greater body mass of stags explains the difference in creatinine concentrations. Only the marginally higher levels of haem and bilirubin in the stalked stags compared with the stalked hinds indicate some degree of stress. By contrast, measures of plasma constituents relating to muscle disruption, red blood cell damage, mobilization of fat reserves and psychological stress differed greatly between hunted and stalked stags, invariably being higher in the hunted group. This evidence does not suggest that rutting activity results in continually elevated stress for stags similar to that imposed by hunting.

However, we question the validity of comparing the welfare of hunted deer with that of rutting stags. Defensive aggression, such as standing to bay, may be elicited by a fear-inducing stimulus (the presence of a predator), whereas competitive aggression is self-generated (Archer 1988). Further, while high testosterone levels may produce a reduction in fear in response to conspecifics (Boissy & Bouissou 1994) it does not necessarily follow that fearfulness will be reduced in other situations. Stags are adapted to cope with the physical demands of the rut, displaying hormonally controlled physical and behavioural changes including decreased tolerance of other males, decreased food intake and preparatory build-up of fat reserves. Since the mating success of stags depends on their fighting ability (Clutton-Brock *et al* 1982, 1988), the risk of injury or death in these circumstances may be seen as an adaptive trade-off favoured by natural selection, rather than an unwanted imposition (Barnard & Hurst 1996). In contrast, deer are not well adapted to the effects of a long chase (Bateson & Bradshaw 1997).

Evidence from blood profiles of injured deer

Comparisons between hunted deer and those injured by poor shooting and other causes are helpful because they provide a basis for relating the state of the hunted animal to those deer that most people would agree are suffering. Hunted deer did not differ from injured deer in measures of muscle disruption (plasma CK, LDH and AST activities) and had higher levels of measures indicating blood damage (plasma haem and bilirubin concentrations). Other measures reflect differences in the activity of hunted and injured groups (although four injured deer killed by the hunt had been chased by hounds prior to being killed, the two with 'old' injuries for some distance). It is notable, however, that cortisol and β-endorphin levels were significantly higher in hunted deer. We conclude that in most of the important groups of indicators of physiological stress, the hunted animals were more stressed than the injured animals.

This has important ramifications for how we regard those deer that escaped from the hunt, the majority of which had run at least the minimum distance covered by a hunted animal that was killed. Clearly, these animals may not have escaped unharmed, contrary to the claims of the supporters of hunting, since those hunted for 5km or more are likely to have sustained damage to their blood and disruption of muscle tissues and, in longer hunts, severely depleted carbohydrate resources. Whether or not such escapees subsequently die from the stressful effects of being hunted has been much debated. We do not know whether deer that escape after being hunted are more likely to die within a few weeks than those that were not hunted, since measuring this effect would have required extensive radio-telemetry studies of hunted deer. Nonetheless, the assertion that deer that escape the hunt do so unharmed cannot be justified without further evidence.

Some indirect evidence of likely effects of hunting on escapees can be gleaned from the literature. 'Capture myopathy', found in wild animals after a prolonged chase or much struggling at the time of capture, has been known for many years in a number of species – including red deer (Jarrett *et al* 1964). This syndrome is not fully understood but is known to be associated with severe stress, two causes of which can be extreme exertion and overheating (Spraker 1993). The possibility that hunting of red deer with hounds may lead to myopathy was suggested by Henshaw and Allen (1989). A large-scale study of white-tailed deer (*Odocoileus virginianus*) in the USA suggested that 12 per cent of them might die within 26 days of capture by rocket net (Beringer *et al* 1996). Delayed deaths may arise from complicating factors such as heart failure, paresis (slight or incomplete paralysis) or paralysis (Bartsch *et al* 1977 and references therein; Beringer *et al* 1996). Additionally, the stress of capture may have suppressed the immune system and put the animals at risk from other causes such as infection (Martin 1997).

It has been argued that if hunted deer routinely died after escaping, Exmoor and the Quantocks would be littered with their carcases. However, if an estimate of 12 per cent mortality is used, based on data from Beringer *et al* (1996), then the total number of hunted deer that escape and die from myopathy or other causes attributable to the effects of having been hunted would only be seven per year over the whole of Exmoor and the Quantocks. Despite the different species and stressor involved, the Beringer *et al* (1996) example serves to illustrate the point that even a relatively high mortality post-hunt would not necessarily result in visible casualties, although descriptions of symptoms observed in some of the disabled deer were not incompatible with this syndrome (Bateson 1997).

Conclusions regarding hunting

Deer in the vicinity of a hunt appear to behave in much the same way as they would towards the presence of a natural predator. We believe that the disturbance resulting from hunting activity is unlikely to constitute a welfare problem for non-target deer. In contrast, hunting is likely to have severe consequences for the welfare of those animals that are the focus of the hunt. The exertion associated with hunting resulted in severe physiological disturbances, many of which appeared seriously maladaptive (Bateson & Bradshaw 1997). This is perhaps unsurprising, given what we know about the evolutionary history and present day behaviour and ecology of this species. Fossil evidence suggests that the cursorial characteristics of deer (long legs, fast running speeds) evolved to reduce transport costs, rather than to equip them to escape predators (Janis & Wilhelm 1993). Hunts with hounds cover much greater distances than hunts by natural pursuit predators such as wolves or coyotes (Murie 1944; Mech 1970; Nelson and Mech 1991; Okarma 1997; Lingle 1998). These rarely chase their prey for more than 1km, whereas the shortest hunt with hounds that led to a kill was 5km and most are considerably longer (Bateson & Bradshaw 1997). Daily movements and seasonal home ranges of red deer are small, even in areas of poor habitat (Clutton-Brock *et al* 1982; Catt & Staines 1987; Carranza *et al* 1991; Strohmeyer & Peek 1996; Langbein 1997). Finally, it appears that red deer, unlike horses, rely much more on panting than on skin evaporation for thermoregulation (Jenkinson 1973). While we have no direct evidence that hunted deer overheat, we believe that the danger of this, particularly to the heavy-bodied autumn stags, is real. Selective brain cooling, for example, can be adversely affected by high sympathetic activity (Jessen *et al* 1994). Overheating may account for many hunts ending in water, and for the apparently dazed behaviour of some hunted deer (Bateson 1997).

In assessing the welfare implications of the physiological responses to hunting found in deer, much has been made of the extreme changes that can be found in elite human and non-human athletes (Harris 1998). We believe that such comparisons are misleading given species differences in physiology, and the effects of training on the ability to cope with the physiological and physical stress imposed by exercise as well as on baseline blood measures (see Saltin *et al* [1977]; Essen-Gustavsson [1986]; Brooks *et al* [1996]). It is notable in this context that, even though the hunt's horses are bred and trained specifically for hunting, hunt staff must change over to fresh mounts part of the way through the day (and hence, often part of the way through a single hunt).

The welfare consequences of stalking

If the welfare cost of hunting is to be compared to that of the alternative culling method, stalking, then it is crucial to have some basis for an objective comparison. Most public concern about stalking relates to wounding rates, particularly when deer may escape wounded. The various methods used to calculate wounding rates gave remarkably consistent results. If the three averages of the proportions of deer killed using two or more shots are weighted by the number of animals involved, the overall mean proportion is 11 per cent. Likewise, the overall mean for the proportion of wounded deer that took more than 2min to die is 7 per cent. These two categories overlap, but not exclusively. Our information from the stalkers is that none of the animals killed with two or more shots took more than 15min to die. The weighted average for the proportion of deer that escaped wounded, based on retrospective and current stalkers' records and analysis of deer carcases, was 2 per cent of the total shot by stalkers.

The wounding frequency obtained with these methods may well be an underestimate, since memories are imperfect and stalkers may not always be aware of when they have wounded an animal. Also, the stalkers who provided us with data were either experienced marksmen or, in the case of amateurs, were accompanied by such. Deer carcases supplied to game dealers typically have had the head removed; therefore, injuries to the head or upper neck resulting from poor shooting would not have been recorded in this part of the analysis. Nevertheless, another approach (see below) gave an identical figure of 2 per cent for the total number of shot animals escaping wounded.

We compared the expected numbers of wounded animals, based on estimates of population size, culling rates by stalkers and wounding rates, with the numbers of wounded and dead animals actually found. A wounding rate of 15 per cent would have resulted in 50 injured deer escaping. The hunts and their followers cover the areas in question quite extensively, and the chances of missing so many injured deer or unexplained carcases are not high – a point commonly employed by the hunting fraternity in rebutting allegations about the likelihood of deer succumbing to myopathy after escaping from the hunts. The calculated 2 per cent wounding rate by stalkers was based on a minimum estimate of the deer population size as being 2500. All our evidence suggests a rate of deer escaping wounded of 2 per cent, very much lower than the 15–45 per cent reported elsewhere (Staines 1985; E Marriage personal communication 1997).

Other welfare-related issues associated with hunting or stalking

The welfare of deer could be compromised by stalking or hunting in ways for which we have no direct evidence. Injuries may be occasionally incurred by deer in fleeing from stalkers or the hunts, but no evidence suggests that the rate of injury is higher with one activity than another. Stalking may cause temporary disruption of larger groups or more permanent changes to group size and activity budgets. Such changes in behaviour could be indicative of a welfare problem (Lewis *et al* 1997). However, it is more likely that red deer adopt different behavioural strategies to cope with the different 'predation' strategies represented by stalking and hunting (Langbein & Putman 1992). The separation of hinds from calves as a result of the disturbance inherent in the culling method is perhaps less likely with stalking than with hunting, since stalking does not involve pursuing a hind with calf for a prolonged period, and the risk of driving the hind outside her normal home range is smaller. Orphaning of calves when the mother is culled is potentially a more serious issue. Many stalkers operate in southwestern England; we do not know what proportion will routinely kill the calf when they shoot the mother, as is recommended practice in Scotland, but we believe that many do not. These differences might occur for a variety of reasons (Langbein & Putman 1992). Clearly, it is easier for stalkers to minimize the welfare problem of orphaning than it is for the hunts.

Comparing the overall consequences of stalking and hunting

All available evidence strongly suggests that hunting with hounds poses a greater welfare problem for individual deer than stalking. In comparing the overall welfare consequences of stalking versus hunting, however, it is important to examine the conditions under which the welfare benefits of reduced hunting might be outweighed by the welfare costs of increased shooting. Were hunting to stop, the number of deer previously killed by hunting would have to be culled by rifle if previous cull numbers were to be maintained. A further consideration is that the proportion of the deer population killed each year might rise if hunting were stopped – as many hunt supporters believe would be the case. Predicting the consequences for welfare can be attempted by the use of simple analytical equations (see Bateson 1997; Bradshaw & Bateson 2000). The advantage of the simple formulation used is that the numbers required to obtain an answer are available and it is not necessary to calculate the units of welfare cost. It has been argued, however, that the effects of wounding are incommensurable with those of hunting (Geist 1997). It is certainly difficult to assert with any confidence just how much worse than hunting is a lingering death after the lower jaw of a deer has been shattered with a rifle bullet.

We have offered some estimates of the relative welfare costs obtained from the physiological measures of hunted deer and seriously wounded deer. While this comparison suggested that the welfare costs of extended hunting and wounding are the same at the moment of assessment, duration of suffering was not considered. In Bradshaw and Bateson (2000), we describe how, if hours of suffering of each individual are considered as separate data points, comparisons may be made between the median number of suffering hours for hunted deer and stalked deer. This statistical approach to the hours of suffering may, however, also be criticized on common sense grounds, since it could be argued that many animals suffering for a short time is equivalent to a few animals suffering for a long time.

Animal welfare implications and conclusions

Disturbance to non-target deer from hunting activity may appear considerable but is likely to be of short duration, and unlikely to raise serious welfare issues. However, the forced chase of red deer, a relatively sedentary species, for average distances exceeding 19km, produces physiological changes that could hardly be more severe in welfare terms. When red deer are hunted with hounds the suffering is likely to be very great. We also consider it likely that this suffering occurs whether or not the deer is eventually killed. While stalking, like hunting, raises a number of potentially serious welfare issues, we believe that wounding is the most important – and it is the only one for which we have evidence. Estimating the frequency with which wounded deer escape is difficult but a figure of 2 per cent is close to the mark. If illicit shooting (poaching), shooting by inexperienced or incompetent stalkers or the use of shotguns increased, the estimate for numbers of deer that escaped wounded would have to be inflated. Even for the experienced stalkers who took part in the study, 11 per cent of deer were not killed with the first shot. It follows that careful management of stalking is important for animal welfare. However, stalking appears to have fewer welfare costs for deer than hunting, and reducing the welfare costs associated with stalking appears more viable than reducing those associated with hunting.

Acknowledgements

This research was commissioned and funded by the National Trust. We thank its staff for their generous support. The study would not have been possible without the cooperation of staff and supporters of the DSSH and QSH, and those stalkers who collected tissue samples and provided cull records. We also thank J Langbein, N Hale and the LACS.

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