CALF SITE SELECTION BY RED DEER (*CERVUS ELAPHUS*) FROM THREE CONTRASTING HABITATS IN NORTH-WEST ENGLAND: IMPLICATIONS FOR WELFARE AND MANAGEMENT

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Abstract *Animal Welfare 1998, 7:* 427-443

This study (1978–93) was concerned with calf site selection by red deer from three contrasting areas (two deer parks and one deer farm) of north-west England. It arose from initial (1960s–70s) concern over poor recruitment and the high incidence of 'abandoned' calves (at one site), and increasing levels of public disturbance in Lyme Park and Tatton Park. A better understanding of calving behaviour could lead to improved management procedures during calving. Habitat selection by adult females was examined indirectly, by recording where calves (0–2 days old) were born in relation to their weight. The deer farm provided a control site, where the effects of their social traditions could be minimized.

Calves were born over a wide area of moorland in Lyme Park but confined to a deer sanctuary in Tatton Park. Areas of obvious plant cover were selected in preference to open ground in Tatton Park and in the deer farm. No marked preferences were apparent in Lyme Park, although some areas were used more frequently than others, over all years. Most calves occurred within female home ranges. In Tatton Park, the heaviest calves were found in the preferred calving sites.

Calf weights varied widely within and between study sites. On average, the smallest (lightest) calves were recorded in Lyme Park and the heaviest in the deer farm. Sex differences in calf weights occurred in Tatton Park, but not at the other two sites. In general, late-born calves were smaller than those born early in the season. Variations in birthweight were linked to differences in female growth and site conditions. In the absence of more detailed statistics, calf weights can provide a useful measure of population performance.

Collectively, these results suggest that red deer can adopt a range of calving behaviours ('tactics') depending on the nature of the habitat (presence or absence of cover), perceived predation 'risks' (levels of disturbance), established social traditions and, possibly, parental investment. Cover appeared to be a primary requirement for calving. In the absence of cover, other behaviours were adopted. In some cases, these behaviours were not in the best

interests of the calf, as parent females rarely returned to feed their calves during the day and often engaged in energetically costly diversionary activities. In deer farms, conflicts between hinds may be exaggerated by limited access to ground cover, similar social status and low variance in calf weights.

In view of these findings, there is a need to devise new ways of attracting captive deer to cover, perhaps by modifications to the habitat mosaic. Observations from Tatton Park show that deer readily use refuges (the sanctuary), when available, although it may be difficult to initiate new behaviours where long-established traditions occur (eg Lyme Park). Mortality amongst calves is unacceptable in deer parks, but further work under more controlled conditions, is required to establish the mechanisms of calf site selection. Effective methods of locating calves are desirable for management purposes.

Keywords: *animal welfare, calving behaviour, deer farms, deer parks, red deer*

Introduction

Although considerable attention has been given to the management of red deer, *Cervus elaphus* L., in Scotland and some areas of lowland Britain (Darling 1937; Lowe 1969; Mitchell *et al* 1977; Clutton-Brock, Guinness & Albon 1982; Ratcliffe 1984; Clutton-Brock & Albon 1989), little research has been carried out in deer parks or farms, where the welfare of deer is of more immediate concern (Hamilton & Blaxter 1980; Humphries *et al* 1989; Langbein & Putman 1992; Pollard *et al* 1992;1993; Bullock *et al* 1993). Deer parks are popular venues for the public and can provide useful models for behavioural research (Bullock & Goldspink 1992).

Red deer conceal their calves for the first few days of life, until they can follow the parent female (Lent 1974; Kelly & Drew 1976). While hiding behaviour probably evolved in response to predation threat (Guinness, Clutton-Brock & Albon 1978; Guinness, Gibson & Clutton-Brock 1978; Nelson & Mech 1981; Lickliter 1984; Shackleton & Haywood 1985; Schwede *et al* 1993), this is difficult to test in Britain because predation is no longer a significant cause of mortality (Guinness, Clutton-Brock & Albon 1978). Nevertheless, calf mortality can be high around birth and late winter both in the wild (Guinness, Gibson & Clutton-Brock 1978; Clutton-Brock, Major *et al* 1987) and in some deer parks and farms (Blaxter & Hamilton 1980; Goldspink 1987). In deer farms, interactions between hinds can increase at calving (Yerex & Spiers 1990). Thus, an improved understanding of calving behaviour might provide a basis for better management of deer and perhaps help to reduce calf mortality (Youngson 1970; Arman 1974; Arman *et al* 1978; Cowie *et al* 1985).

Red deer occur across a wide range of habitats in Britain (de Nahlik 1987; Putman 1988). However, calving behaviour which is effective under woodland cover, might be inappropriate on open sites. The need to suckle the calf, is at variance with the needs of concealment (Hirth 1977; Byers & Byers 1983; Carl & Robbins 1988). Habitat conditions at birth could be an important factor influencing reproductive success in red deer, as for other animals (Barrett 1981; Kelly & Drew 1976; Jackson *et al* 1988).

Reproduction is energetically costly for mammals (Cockerill 1982; Clutton-Brock, Albon & Guinness 1982; Clutton-Brock *et al* 1983;1989; Pollard *et al* 1992; Laurenson 1995). If the costs of caring (suckling plus defence) for the current year's young adversely affect future prospects of reproduction, the female might 'chose' to abandon the calf (Trivers 1985; Smith 1987; Festa-Bianchet 1989; Clutton-Brock 1991; Caro *et al* 1995) depending on social

rank (Thouless & Guinness 1986; Clutton-Brock *et al* 1989; Kojola 1989; Fouda *et al* 1990; Freeman *et al* 1992; Green & Rothstein 1993; Meikle *et al* 1993).

In this study (1978-1993), we examined calf site selection in red deer from two contrasting deer parks and one deer farm. The study arose out of concern over the poor breeding performance (natality) and high incidence of apparently abandoned calves in Lyme Park (Goldspink 1987). Both parks have suffered increased levels of public disturbance since the 1960s. The study forms part of more detailed investigations into behaviour of deer during the first year of life (Gibson 1994; Holland 1995).

Materials and Methods

Study sites

The study was carried out in two Cheshire deer parks and one private deer farm (Table 1) between 1978 and 1993. Both parks have contained deer for over 500 years and been managed by culling (Whitehead 1964).

Table 1 Location and population characteristics of red deer in the three study sites.

Site location and date of opening	Area (km^2) and altitude (m)	Number of deer	Number of hind home ranges and local density per km^2	Median calving date		
				Both sexes	Male	Female
Lyme Park *53° 20.5'N, 2°3'W 1947*	5.35 (450m)	250-300	3 36-77	10 June	-	-
Tatton Park *53° 19.5'N, 2°22'W 1969*	250 (150m)	200	1[1] na	16 June	13 June	20 June
Deer farm *53° 20'N, 2°23'W 1981*	17 (160m)	100-150	c 100	20 June	21 June	13 June

[1] Under study

Lyme Park (53°20.5'N, 2°3.0'W) is situated to the south of the Pennine anticline (Figure 1) and contains open moorland to 400m altitude. Vegetation consists of mixed stands of *Molinia caerulea, Deschampsia flexuosa* and *Juncus effusus* in various stages of succession (Latusek 1983). Hinds occur in three main areas of Lyme Park (the Park, Park moor and Cluse Hay) but rarely move between natal home ranges (Holland 1995). A sandstone ridge acts as a natural division between the moor and Cluse Hay regions (Figure 1). Deer densities are highest on the moorland (Goldspink 1987).

Tatton Park (53°19.5'N, 2°22.0'W) is a lowland park (Cantor 1989) made up of a mosaic of rough pasture and small woodlands (Birkett 1994). Deer have access to a sanctuary to the north of the park (Figure 2). Stags remain spatially separated from hinds (Clutton-Brock, Iason & Guinness 1987) in both parks, except during the rut. Rutting serves to initiate and synchronize oestrus behaviour in hinds (Estes 1976; McComb 1987).

The deer farm (53°20.0'N, 2°23.0'W; Figure 3) was established in 1981 and stocked with hinds for moderate (Fletcher 1989) levels of production. Calves are weaned at various ages (months) depending on market demand. No attempt is made to grade yearling hinds by size, or manipulate hind stocks for breeding (Yerex & Spiers 1990).

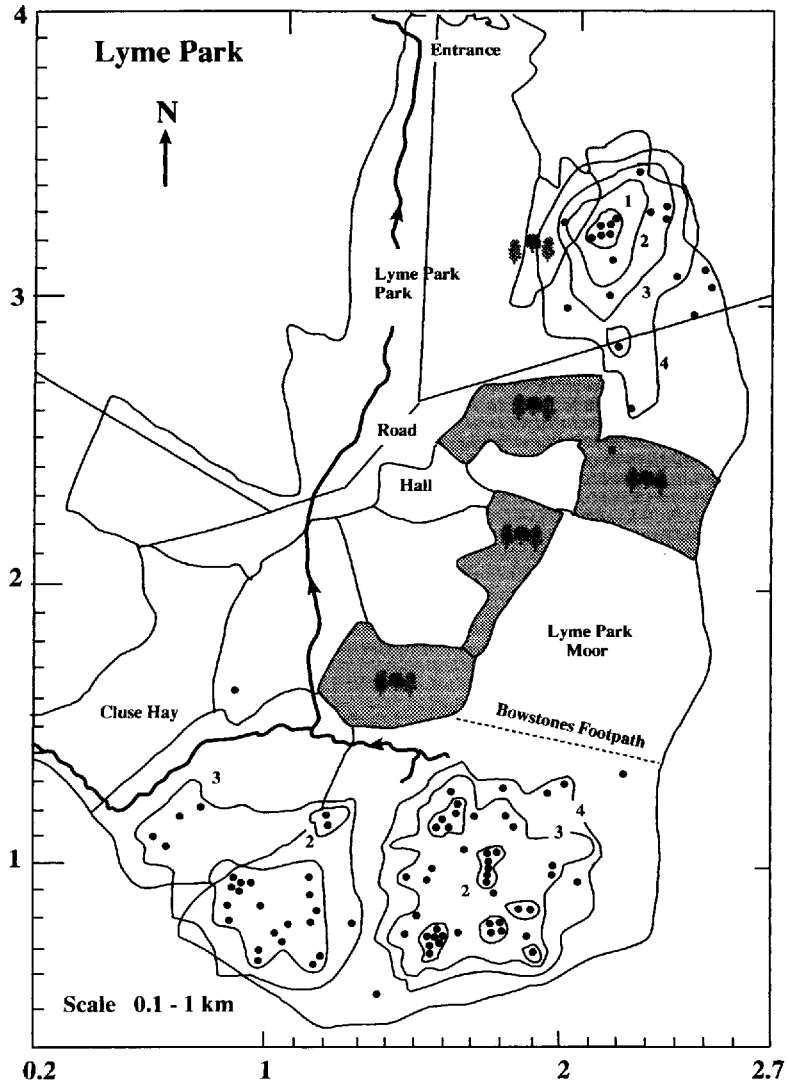

Figure 1 **Map of Lyme Park, showing the distribution of calving (0-2 days old) sites across three hind home ranges (data pooled over all years). Streams (arrowed lines) and woodlands (shaded) are indicated. Contours labelled 1, 2, 3 and 4 refer to local aggregations of calves as defined by harmonic mean distances (100m increments) see, *Methods*. A footpath crosses the moor from the highest point at Bowstones. The grid overlay is taken from the Ordnance Survey Map.**

Methods

Observations on calving behaviour began during the summer of 1978 in Lyme Park and continued until the mid 1990s. The study was extended to include Tatton Park and the deer farm in 1986, in an attempt to evaluate the possible role of parental investment (calf weight) on calf site selection (Clutton-Brock, Iason *et al* 1982; Clutton-Brock *et al* 1983; Fouda *et al* 1990).

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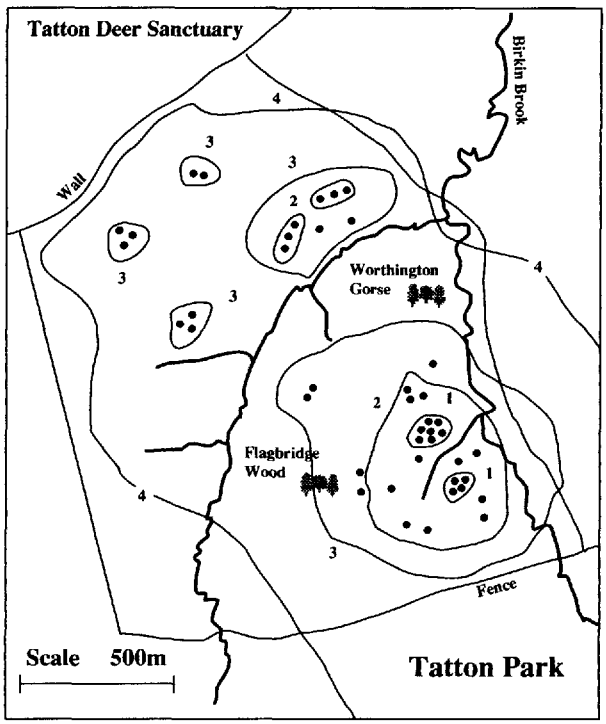

Figure 2 **Tatton Park deer sanctuary showing the distribution of calving (0-2 days old) sites in 1986. Tributaries of the Birkin Brook (flowing north) indicated as a dark line. Contours labelled 1, 2, 3 and 4 refer to local aggregations of calves as defined by harmonic mean distances (100m increments) see, *Methods*. Scale taken from the Ordnance Survey map. Arbitrary origin (x=0, y=0) at the left hand corner of the figure.**

Calves were located (0400h–0900h) by direct observation of suckling hinds (Guinness *et al* 1979), or by sampling techniques based on random, systematic or area-restricted search (Holland 1995), to mimic hypothetical, predator behaviours. Calves were aged, weighed, sexed and ear-tagged, where appropriate. A few (n = 12) calves were fitted with small radio tags to monitor changes in movement with age (Gibson 1994; Holland 1995). The age assessments (days since birth), were based on calf behaviour, hoof hardness and condition of the umbilicus (Mitchell 1971).

Animals were located by triangulation and recorded as grid coordinates (on the Ordnance Survey – British National Grid). Cover characteristics were noted for each calf site and estimates of vegetation area made from aerial photographs (Latusek 1984) or by direct survey (Birkett 1994). Calf ranges were determined retrospectively, from spot locations (1978-1993) of tagged animals (Goldspink 1987), or directly by radio-telemetry (Gibson 1994; Holland 1995). Natality (net calf production) was estimated (each year) by a field census in late August. The distribution of calving sites was described by harmonic mean 'distances', calculated (in 10-100 m increments) using a simple BASIC routine, to all calf locations (Dixon & Chapman 1980). Contours or isopleths, were drawn by connecting points of equal (1–4) value, or by interpolation.

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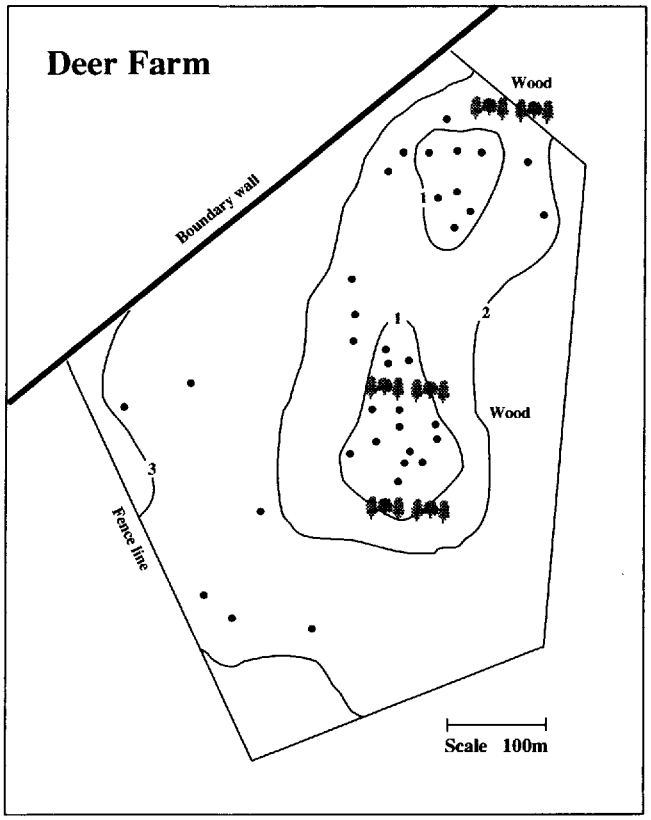

Figure 3 **Deer farm showing the distribution of calving (0-2 days old) sites in 1986. Contours labelled 1, 2 and 3 refer to local aggregations of calves as defined by harmonic mean distances (10m increments) see, *Methods*. Scale taken from the Ordnance Survey map. Arbitrary origin (x=0, y=0) at the left hand corner of figure. Scattered trees indicated (wood) within paddock.**

Fieldwork was subject to a strict code of practice laid down by the park managements. In Lyme Park, hind home ranges were visited in rotation. Calves were left undisturbed during cold or wet weather. As the calf site is initially selected by the parturient hind, the following results are restricted to animals up to a maximum of 2 days old. The behaviour of older calves (Suttie 1983) is considered elsewhere (Holland 1995). Observations on hind and calf behaviour were made from woodland cover, adjacent to hind home ranges (Gibson 1994).

Statistical analysis

Calf site preferences were examined by comparisons of observed distributions with those expected on the basis of percentage cover of each vegetation/habitat type. Tests were based on the *G*-test or chi-squared test, depending on sample sizes (Sokal & Rohlf 1981). Comparisons of calf weights were based on parametric tests (two-tailed), where appropriate. Variation in calf weights was described by the coefficient of variation (the standard deviation/mean). For analyses, the unit of sampling effort was standardized as two people searching for 5h.

Results

Ease of locating calves

Calves (0–2 days old) were difficult to locate in Lyme Park. There was no apparent improvement in location rates (mean numbers per unit effort) during the study ($r = 0.02$, $df = 12$, $P > 0.05$), or in the numbers (relative to those born) found on different calving areas (chi-square = 1.09, $df = 2$, $P > 0.05$). No one method of locating calves (see, *Methods*) was more successful than any other. The average time to find calves varied from 30min to over 4h, between sampling occasions.

Calves were easier to locate in Tatton Park than Lyme Park, but there was no significant improvement in locations per unit of effort over the calving season ($r = - 0.012$, $df = 28$, $P > 0.05$). The average time taken to find a male calf (mean = 25.5min) was similar to that (mean = 22.9min) for a female calf ($t = 0.65$, $df = 26$, $P > 0.05$). Calves were readily located within the deer farm.

Spatial distribution of calving sites

In Lyme Park, most calves were located within one of three hind home ranges (Figure 1). No calves were found in areas to the north of the Bowstones footpath and only occasionally within woodland cover (Figure 1). Calves were widely dispersed across hind home ranges, in any one year. However, if data are pooled over all (1978-93) years, some sites were used more often than others (Table 2 and Figure 1). In some cases (moor and park), these areas (highlighted by the 200m isopleth) were associated (P values for the two study periods: $P = 0.001–0.037$) with patches of *Juncus;* but no obvious association was apparent on Cluse Hay (P values for the two study periods: $P = 0.1155 –0.170$). See Table 3.

Table 2 **Cumulative number and percentage of deer calves (0-2 days old) located within each isopleth zone (increment 100m) in Lyme Park (1978-1988), Tatton Park (1986) and the deer farm (1986).**

Site	Isopleth bounday					Total location
	100m	200m	300m	400m	>400m	
Lyme Park						
Park	-	7	14	17	21	21
Per cent		33.3	66.6	80.1	100	
Moor	-	25	43	46		46
Per cent		54-35	93.5	100		
Cluse Hay	-	21	26			26
Per cent		80.77	100			
Tatton Park	11	29	43			43
Per cent	25.58	67.44	100			
Deer farm	20	28	34			34
Per cent	58.32	82.35	100			

In Tatton Park, all calves occurred within the deer sanctuary (Figure 2). Most were found within plant cover provided by ragwort, *Senecio jacobaea*, or rushes, *Juncus* spp., defined by the 100m and 200m isopleths (Table 4a). Open grassland and trees were avoided ($P < 0.01$). In terms of topography, level ground was selected in preference ($P < 0.05$) to stream valleys and hollows (Table 4b).

Table 3 **Numbers of calves (0-2 days old) located within *Juncus* and non *Juncus* dominated vegetation in three areas of Lyme Park between (a) 1978-1988 and (b) 1989-1993. (Expected values were calculated from relative contributions of each vegetation type per area.)**

a)	*Juncus*	Non *Juncus*	Total	G statistic/*P* value
Park				
Observed	6	15	21	
Expected	0.24	20.76		28.91/< 0.05
Moor				
Observed	25	21	46	
Expected	3.91	42.09		63.57/< 0.01
Cluse Hay				
Observed	0	26	26	
Expected	1.67	24.33		2.43/> 0.05
Total all sites	31	62	93	
b)				
Park	no data	no data	no data	no data
Moor				
Observed	4	11	15	
Expected	1.28	13.73		4.28/> 0.05
Cluse Hay				
Observed	0	1	1	
Expected	0.06	0.94		5.62/> 0.05
Total all sites	4	12	16	

Table 4 **Number of calves (0-2 days old) found in each of four habitat types in Tatton Deer Park (a and b) and the deer farm (c).**

a) Tatton habitat/vegetation

	Open grass	*Senecio jacobaea*	*Juncus*	Trees	Total	G statistic/*P* value
Observed	9	10	8	1	28	
Expected	18.2	4.2	2.24	3.36		22.62/< 0.01

b) Tatton topography/vegetation

	Stream valley	Hollows	Open ground	Trees	Total	G statistic/*P* value
Observed	0	0	27	1	28	
Expected	2.52	0.56	21.56	3.36		9.04/< 0.05

c) Deer farm – habitat/vegetation

	Grass	*Cirsium arvense*	*Urtica dioica*	Trees	Total	G statistic/*P* value
Observed	5	5	3	16	29	
Expected	22.33	0.58	0.29	5.8		51.21/< 0.0001

A similar preference for cover was apparent in the deer farm (Figure 3), where thistles, *Cirsium arvense,* nettles, *Urtica dioica,* and fallen branches below the trees were utilized ($P < 0.001$; Table 4c). Other areas of the paddock were largely avoided.

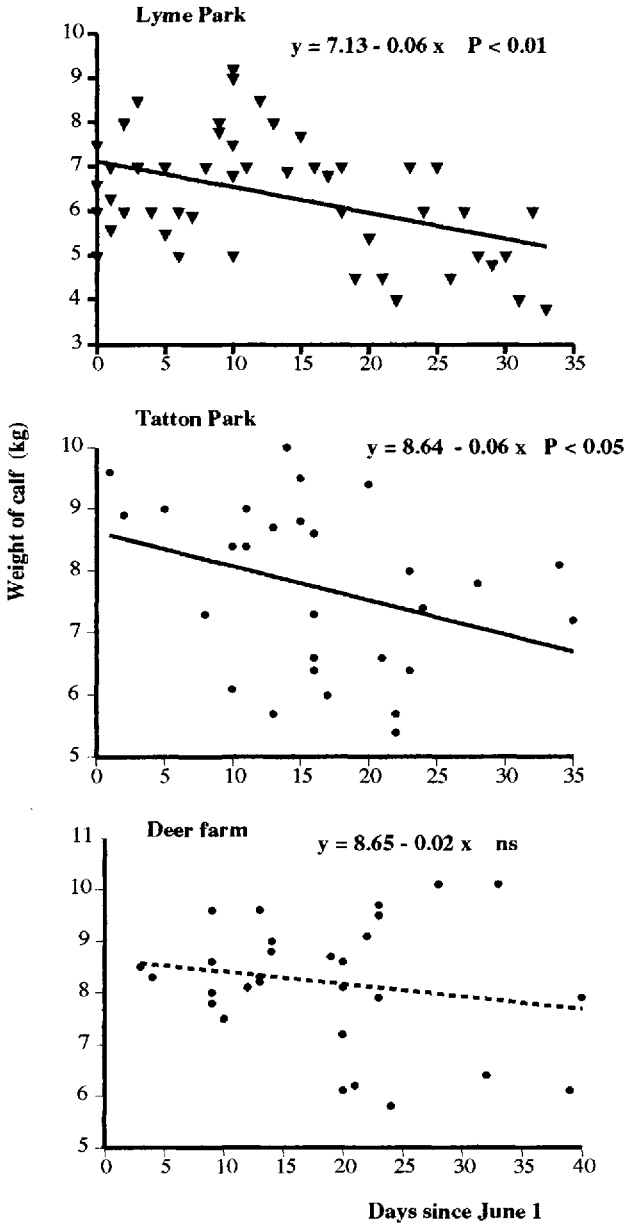

Figure 4 **Weight of calves (0-2 days old) recorded in (a) Lyme Park (b) Tatton Park and (c) the deer farm during the calving period. Data (by sex and by year) pooled. The dashed line (trend) for the deer farm, although not significant, is included as for comparison. *P* values are indicated.**

Calf weights and date of birth

Over 200 calves (0–2 days old) were located during the study (all sites), of which 106 were weighed and sexed. Median calving dates varied from 10 June in Lyme Park to 20 June at the deer farm (Table 1). Individual calf weights varied from 4.3–10.1 kg, across sites. Mean weights (pooled by sex), ranged from 6.4kg in Lyme Park to a maximum of 8.2kg in the deer farm ($F_{2,105}$ = 20.82, $P < 0.001$; Table 5). The smallest (lightest) calves occurred in Lyme Park (t = 3.37, df = 46, P = 0.002) and the largest in the deer farm (Table 5). Male calves were, on average, heavier than female calves in Tatton Park (t = 2.54, df = 19, P = 0.02) but not in the deer farm ($P > 0.05$). Data from Lyme Park were equivocal (Goldspink 1987). Early-born calves were generally heavier than late-born calves in Lyme Park and Tatton Park, but not in the deer farm (Figure 4). The overall range in calf weights was highest in Lyme Park and lowest in the deer farm (coefficient of variation, on mean calf weight across sites r_S = - 0.75, df = 8, P = 0.0199 , Table 5).

Table 5 **Mean calf weight from the two deer parks and the deer farm. Data are given for sexes and home ranges where available.**

Location	Mean calf weight (kg)	Sample size	Coefficient of variation	Significance
*1) **Deer farm***	8.2	29	0.148	
Males	8.24	14	0.174	
Females	8.16	15	0.126	ns
*2) **Tatton Park***	7.73	28	0.175	
Males	8.48	11	0.155	t = 2.54
Females	7.25	17	0.155	P = 0.02
*3) **Lyme Park***	6.36	49	0.211	
Moor	5.78	25	0.202	t = 3.37
Park	6.96	24	0.18	P = 0.002

Between sites (1, 2, 3) sexes combined $F_{2,105}$ = 20.82, $P < 0.001$

Parental investment

Mean calf weights (Table 6) varied between cover types in Tatton Park ($F_{2,24}$ = 4.20, $P <$ 0.05) but not in the deer farm ($F_{2,23}$ = 2.19, $P > 0.05$). The heaviest calves occurred in the preferred calving sites (ranked by frequency of use) in both the deer park (t = 2.16, df =19, P < 0.05) and the deer farm (t = 3.30, df = 3, $P < 0.05$), respectively (Table 6). However, there was no apparent difference in the sex ratio of calves in the different cover classes in Tatton Park (chi-square = 1.37, df = 2, $P > 0.05$), or in the deer farm (chi-square = 0.04, df = 2, $P >$ 0.05). Similarly, there was no apparent effect of date, on the use of cover in the Tatton sanctuary (Wald-Wolfowitz runs test Z = 1.46, $P > 0.05$), or the deer farm (Z = 0.27, $P >$ 0.05). Early-born calves (prior to median date of calving) were as likely to be found in preferred calving sites, as late-born (after median date) calves (chi-square = 2.2, df =1, $P >$ 0.05).

Discussion and management implications

Context

Management of wild Scottish deer is usually based on an assessment of performance and site conditions (Mitchell *et al* 1977). Typically, growth rate and natality decline with population

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Table 6 **Mean weight (kg) of calves found in each habitat class, ranked by frequency of use, in Tatton Park enclosure and the deer farm.**

Site	Calving area ranked by frequency of use[1]			
Tatton Park	1	2	3	Total
Mean calf weight	7.8	6.4	8.2	
Number	16	6	5	27
Range	6.5-10.0	5.4-8.9	6.4-9.0	
Sex ratio male: female	5:11	3.3	2.3	
Deer farm				
Mean calf weight	8.2	7.8	9.3	
Number	13	10	4	27
Range	5.8-10.1	6.1-10.1	8.8-9.7	
Sex ratio male: female	6.7	5.5	2.2	

[1] 1 = site where most births were recorded

density although, research on the Isle of Rhum has shown that both can be modified through social behaviour (Clutton-Brock, Iason & Guinness 1987; Clutton-Brock, Major *et al* 1987). In terms of welfare in deer parks, it is the individual response to disturbance that is of most concern to Management. Langbein and Putman (1992) could find no obvious effects of disturbance on performance in their study (involving time budget analyses of maintenance behaviours) on park deer, although as a cautionary note they suggested that 'disturbance might effect natality, through its effect on perinatal mortality, where mothers are disturbed immediately after parturition before they have a chance to bond with their new offspring'. Calf site selection in red deer, is a compromise between the needs of concealment (Clutton-Brock & Guinness 1975; Estes 1976; Barrett 1981), and the need to develop of an effective suckling response (Lent 1974; Guinness *et al* 1979; Kallquist & Mossing 1982; Brownlee 1986; Fouda *et al* 1990).

Within the restricted range available in deer parks, disturbance during the first 2 days of life could be critical for the future prospects of the calf. Energetically costly, diversionary tactics are often adopted by adult hinds during this period (Yahner 1980; Carl & Robbins 1988; Bergerud *et al* 1990; Caro *et al* 1995). In this study, we have attempted to extend the scope of research to include the role social behaviour (Festa-Bianchet 1989) and tradition on calving behaviour. On Rhum, mortality during the first year of life can reach 37 per cent of calf production (Lowe 1969).

Date of conception and calf weights

Calves were born over a period of about 40 days across all the sites (Figure 4). A similar range of calving dates has been recorded for Scottish deer, reflecting the timing of the rut, condition of the hinds and gestation periods. In Glenfeshie, yeld hinds (those without a dependent calf at the time of the rut) were found to conceive slightly earlier (median date = 15 October) compared with milk hinds (median date = 20 October; Mitchell & McCown 1986). On Rhum, gestation times varied from a mean of 234.2 to 236.1 days for male and female calves, respectively (Guinness, Gibson & Clutton-Brock 1978). Observed variations in calving dates recorded during the current study cannot be fully explained (Table 1), but may reflect differences in timing of the rut between sites, variation in the proportions of yeld hinds and progression of oestrus.

Mean calf weights ranged from 6.4kg in Lyme Park to a maximum of 8.2kg in the deer farm (Table 5). Weights from Lyme Park were similar to those recorded for male (mean =

6.7kg, n = 73) and female (mean = 6.24kg, n = 70) calves at Glenfeshie (Mitchell 1971; Mitchell & McCowan 1986) and on Rhum (6.9kg and 6.4kg, respectively; Guinness, Clutton-Brock & Albon 1978). Calf weights in the deer farm were high by comparison, but similar to those recorded for male and female calves (mean = 9.0kg and 8.5kg, respectively, n = 280), in some farms (Gibson 1994).

There can be little doubt that these differences in calf weights reflect the size, growth and age compositions of the three hind populations studied. Growth rates of hinds in Lyme Park, are unexceptional for this species in the UK (Goldspink 1987), but those in the deer farm are high. Hinds achieve their asymptotic weights at an early age in the deer farm (T Birtles unpublished data). These differences were matched by the calf:hind ratios across sites, ranging from 0.5 in Lyme Park to 0.7 in the deer farm. On Scottish sites, calf:hind ratios vary from 0.23–0.51 (Mitchell *et al* 1977;Guinness, Clutton-Brock & Albon 1978; Mitchell & McCowan 1986).

In addition, the overall variance in calf weights increased across sites, with those in Lyme Park having the largest coefficient of variation (Table 5). This suggest that the three populations experience different patterns of selection. Whilst selection in the deer farm is likely to be directional, that in the deer parks may be more disruptive, as a result of the stochastic effects of culling, in small populations.

Calves born early in the season were generally heavier than those born late in the season, except at the deer farm (Figure 4). Studies on Rhum have shown that calves born to young hinds are generally lighter than those born to older, more experienced hinds and often suffer high summer mortality. By contrast, late-born calves of mature hinds are more likely to suffer winter mortality (Guinness, Clutton-Brock & Albon 1978; Guinness, Gibson & Clutton-Brock 1978; Sibbald *et al* 1993), through social exclusion from good winter grazing. Similar effects have been recorded for other ungulate species (Green & Rothstein 1993).

Calf site selection

A wide range of calving behaviours was recorded during the study. In the absence of obvious disturbance, hinds preferred to calve within ground cover provided by rushes or other tall plants. In some cases, this resulted in local concentrations of calves in certain areas of Tatton Park deer sanctuary (Figure 2) or, in the case of the deer farm, the paddock (Figure 3). These differences are manifest as the number of calves contained within isopleths of the same value. Surprisingly, woodland cover was avoided in the sanctuary, perhaps because of a preference for open ground where occasional human incursions could be monitored by the hind. In this context, it is interesting to note that hinds avoided low-lying ground, within stream valleys. Since hinds can protect their calves through diversionary activities, early warning of approaching danger is clearly an advantage. On Rhum, hinds generally calved outside the normal limits of their home range boundaries (Guinness *et al* 1979).

In Lyme Park, calves were born over a wide area of hind home ranges on the moorland region (Figure 1). No obvious patterns in calf site selection were apparent, although certain areas were used more frequently than others over all years. Taken together, these results suggest that deer can adopt a range of calving tactics (Bergurud *et al* 1990), depending on the nature of the habitat, perceived disturbance (potential predation threat), long-standing spatial and social traditions and/or competition for limited calving sites. Although we devised various methods for locating calves in Lyme Park, none were particularly successful (excluding the direct observation of suckling hinds). This suggests, that the concealment tactic employed by deer in Lyme Park is 'successful' in the short term.

Parental investment

Most of the results concerning the effects of parental investment on calf site selection were inconclusive, except that larger calves were more likely to be found in the preferred calving habitat in the deer sanctuary. This suggests the large hinds, which calve early in the season, may have a competitive advantage over smaller hinds, which calve later. Unfortunately, the effect of calving time could not be confirmed, because of the limited data available. Nevertheless, in Lyme Park, calves born to young hinds late in the season are likely to occur (perhaps through social exclusion) in peripheral areas of home ranges, and be more susceptible to public disturbance, as all home ranges are bounded by public footpaths. Small, late-born calves are particularly vulnerable.

Management

Management of deer parks is subject to a number a constraints. At present most management decisions are based on measures of performance, such as the calf:hind ratios or sex ratios at birth (Meikle *et al* 1993). Unfortunately, these can only provide crude indices of performance, and cannot take into account calf mortality during the summer or winter periods. In most cases, more detailed measures of performance are ruled out, either by manpower or by costs. Our study suggests that the monitoring of calf weights is a useful surrogate for more extensive data on growth rates. However, in order to monitor calves it is necessary to locate them effectively. In Lyme Park, this is not possible, largely because of a continuing conflict (ie arms race) between the needs of the deer for concealment and the obvious intrusion required to locate them. These behaviours have developed over the years, through social traditions, during a long period of residence in the park. Interestingly, the results for the two other sites suggest that where these traditions can be overcome, deer will calve in a more confined space, so long as cover is available. This is likely to be the instinctive pattern among red deer, since no social traditions are possible within the deer farm

Animal welfare implications

Calving is a critical period in the life of deer. In deer parks this is compounded by restrictions of space, long-established social traditions and, in some cases, increasing public disturbance (Goldspink 1987; Humphries *et al* 1989; Langbein & Putman 1992; Bullock *et al* 1993). In terms of management, culling regimes can be disruptive because of difficulties of selecting hinds by age class and reproductive status (yeld versus milk), and the uncertain role of social structures in deer parks. In the absence of habitat mosaic and ground cover, our results suggest that the calving behaviours may not always be in the best interests of the calf. In some situations, calving behaviours may lead to increased exposure to public disturbance, especially in peripheral areas of home ranges. In addition, inappropriate behaviours may be adopted by nursing hinds.

Detailed observations by Gibson (1994) and Holland (1995), suggest that hinds avoid suckling their newborn calves during the day, under open conditions. While the reduced milk intake may be compensated for by some increase in consumption at night, this is unlikely to enhance the survival prospects of calves during cold or wet weather. Apparent rejection of the calf is likely to lead to public intervention if calves are found close to footpaths. Furthermore, hinds with newborn calves will adopt energetically costly diversionary tactics if disturbed (Gibson 1994;Holland 1995), which by any criteria, must be viewed with some concern.

Even in deer farms, more research is required to understand the role of social behaviour in calving behaviour. Through selection for high growth rates, most hinds are of a similar size

and social status which may lead to intense competition for limited calving sites. Competition could be further exaggerated by a low variance in calf weights in such sites. The results from Tatton Park show that deer will adapt, with time, to calving in more secure sites, if cover is available and if public access is restricted. However, even in this situation, a high variance in calf weights suggests that direct intervention may be necessary for small, late-born calves.

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References

Arman P 1974 A note on the parturition and maternal behaviour of captive red deer (*Cervus elaphus L.). Journal of Reproduction and Fertility 37:* 87-90

Arman P, Hamilton W J and Sharman G A M 1978 Observations on the calving of free ranging tame red deer (*Cervus elaphus* L.). *Journal of Reproduction and Fertility 54:* 279-283

Barrett M W 1981 Environmental characteristics and functional significance of pronghorn fawn bedding sites in Alberta. *Journal of Wildlife Management 45:* 120-131

Bergerud A T, Ferguson R and Butler H E 1990 Spring migration and dispersion of woodland caribou at calving. *Animal Behaviour 39:* 360-369

Birkett A 1994 *Reproductive Behaviour and Mating Strategies of Fallow Deer in an Enclosed Deer Park.* Unpublished PhD thesis, Manchester Metropolitan University, UK

Blaxter K L and Hamilton W J 1980 Reproduction in farmed red deer, calf growth and mortality. *Journal of Agricultural Science, Cambridge 95:* 275-284

Brownlee A 1986 The value of the new-born calf in ethological studies. *Applied Animal Behavioural Science 16:* 91-92

Bullock D J and Goldspink C R 1992 *Management, Welfare and Conservation of Park Deer. Proceedings of the Second Deer Parks Symposium, Leicester.* Universities Federation for Animal Welfare: South Mimms, UK

Bullock D J, Kerridge F J and Hanlon A and Arnold R W 1993 Short-term responses of deer to recreational disturbance in two deer parks. *Journal of Zoology 230:* 327-332

Byers J A and Byers K Z 1983 Do pronghorn mothers reveal the locations of their hidden fawns? *Behavioral Ecology and Sociobiology 13:* 147-156

Cantor L 1989 English Deer Parks, an Historical Background. In: Baxter-Brown M and Goldspink C R (eds) *Management, Conservation and Interpretation of Park Deer* pp 1-5. British Deer Society: Pangbourne, UK

Carl G R and Robbins C T 1988 The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. *Canadian Journal of Zoology 66:* 239-246

Caro T M, Lombardo L, Goldizen A W and Kelly M 1995 Tail-flagging and other antipredator signals in white-tailed deer: new data and synthesis. *Behavioural Ecology 6 (4):* 442- 450

Clutton-Brock T H 1991 *The Evolution of Parental Care.* Princeton University Press: Princeton, USA

Clutton-Brock T H and Albon S D 1989 *Red Deer in the Highlands.* Blackwell Scientific: Oxford, UK

Clutton-Brock T H, Albon S D and Guinness F E 1982 Competition between female relatives in a matrilocal mammal. *Nature 300:* 178-180

Clutton-Brock T H, Albon S D and Guinness F E 1989 Fitness costs of gestation and lactation in wild mammals. *Nature 337:* 260-262

Clutton-Brock T H and Guinness F E 1975 Behaviour of red deer (*Cervus elaphus* L.) at calving time. *Animal Behaviour 55:* 287-300

Clutton-Brock T H, Guinness F E and Albon S D 1982 *Red Deer: the Behaviour and Ecology of Two Sexes.* University of Chicago Press: Chicago, USA

Clutton-Brock T H, Guinness F E and Albon S D 1983 The costs of reproduction to red deer (*Cervus elaphus* L.) hinds. *Journal of Animal Ecology 52:* 367-383

Clutton-Brock T H, Iason G R, Albon S D and Guinness F E 1982 Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. *Journal of Zoology 198:* 227-236

Clutton-Brock T H, Iason, G R and Guinness F E 1987 Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cervus elaphus). Journal of Zoology 211:* 275-289

Clutton-Brock T H, Major M, Albon S D and Guinness F E 1987 Early development and population dynamics of red deer. I: Density dependent effects on juvenile survival. *Journal of Animal Ecology 56:* 53-69

Cockerill R A 1982 *Functional Aspects of Mother-offspring Relationships in Red Deer.* Unpublished PhD thesis, University of Cambridge, UK

Cowie G M, Morre G H, Fisher M W and Taylor M J 1985 Calving behaviour of farmed red deer. In: Reitson N S, Wilson P R (eds) *Proceedings of Deer Course for Veterinarians pp 143-154.* New Zealand Veterinary Association, Deer Branch: Ashburton, New Zealand

Darling F F 1937 *A Herd of Red Deer.* Oxford University Press: London, UK

de Nahlik A J 1987 *Wild Deer: Culling, Conservation and Management.* Ashford Press: Southampton, UK

Dixon K R and Chapman J A 1980 Harmonic mean measure of animal activity. *Ecology 61:* 1040-1044

Estes R D 1976 The significance of breeding synchrony in the wildebeest. *East African Wildlife Journal 14:* 135-152

Festa-Bianchet M 1989 Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis). Journal of Animal Ecology 58:* 785-795

Fletcher T J 1989 Suggestions for deer park managers from a deer farmer. In: Baxter-Brown M and Goldspink C R (eds) *Management, Conservation and Interpretation of Park Deer* pp 60-66. British Deer Society: Pangbourne, UK

Fouda M M, Nicol C J, Webster A J F and Metwally M A 1990 Maternal-infant relationships in captive sika deer (*Cervus nippon). Small Ruminant Research 3:* 199-209

Freeman L C, Freeman S C and Romney A K 1992 The implications of social structure for dominance hierarchies in red deer, *Cervus elaphus* L. *Animal Behaviour 44:* 239-245

Gibson S D 1994 *A Comparative Study on the Behaviour and Ecology of Red Deer* (Cervus elaphus L.) *During the First Year of Life.* Unpublished PhD thesis, Manchester Metropolitan University, UK

Goldspink C R 1987 The growth, reproduction and mortality of an enclosed population of red deer (*Cervus elaphus* L.) in north-west England. *Journal of Zoology 213*: 23-44

Green W C H and Rothstein A 1993 Persistent influences of birth date on dominance, growth and reproductive success in bison. *Journal of Zoology 230*: 177-186

Guinness F E, Clutton-Brock T H and Albon S D 1978 Factors affecting calf mortality in red deer (*Cervus elaphus). Journal of Animal Ecology 47*: 817-832

Guinness F E, Gibson R M and Clutton-Brock T H 1978 Calving times in red deer (*Cervus elaphus). Journal of Zoology 185:* 105-114

Guinness F E, Hall M J and Cockerill R A 1979 Mother-offspring association in red deer (*Cervus elaphus* L.) on Rhum. *Animal Behaviour 27:* 536-544

Hamilton W J and Blaxter K L 1980 Reproduction in farmed red deer 1. Hind and stag fertility. *Journal of Agricultural Science, Cambridge 95:* 261-273

Hirth D H 1977 Social behaviour of white-tailed deer in relation to habitat. *Wildlife Monographs 53:* 1-55

Holland R K 1995 *Social Behaviour, Dispersion and Dispersal of Red Deer (*Cervus elaphus L.*) During the First Two Years of Life.* Unpublished PhD thesis, Manchester Metropolitan University, UK

Humphries R E, Smith R H and Sibly R M 1989 Effects of human disturbance on the welfare of park fallow deer. *Deer 7:* 458- 63

Jackson S L, Hik D S and Rockwell R F 1988 The influence of nesting habitat on reproductive success of the lesser snow goose. *Canadian Journal of Zoology 66:* 1699-1703

Kallquist L and Mossing T 1982 Olfactory recognition between mother and calf in reindeer **(***Rangifer t. tarandus* L.*). Applied Animal Ethology 8:* 561-565

Kelly R W and Drew K R 1976 Shelter seeking and suckling behaviour of the red deer **(***Cervus elaphus)* calf in a farmed situation. *Applied Animal Ethology 2:* 101-110

Kojola I 1989 Mother's dominance status and differential investment in reindeer calves. *Animal Behaviour 38:* 177-185

Latusek E P 1983 *The Autecology of* Molinia caerulea *(L) Moench. with Particular Reference to Grazing.* Unpublished PhD thesis, Manchester Polytechnic, UK

Langbein J and Putman R J 1992 Behavioural responses of park red and fallow deer to disturbance and the effects on population performance. *Animal Welfare 1:* 19-38

Laurenson M K 1995 Behavioural costs and constraints of lactation in free-living cheetahs. *Animal Behaviour 50:* 815-826

Lent P C 1974 Mother-infant relationships in ungulates. In: Geist V and Walther F (eds) *The Behaviour of Ungulates and its Relation to Management* pp 14-55. International Union for the Conservation of Nature and Natural Resources: Gland, Switzerland

Lickliter R E 1984 Hiding behaviour in domestic goat kids. *Applied Animal Behavioural Science 12:* 187-192

Lowe V P W 1969 Population dynamics of the red deer (*Cervus elaphus*) on Rhum. *Journal of Animal Ecology 38:* 425-456

McComb K 1987 Roaring by red deer stags advances the date of oestrus in hinds. *Nature 330:* 648-649

Meikle D B, Drickamer L C, Vessey S H, Rosenthal T L and Fitzgerald K S 1993 Maternal dominance rank and secondary sex ratio in domestic swine. *Animal Behaviour 46:* 79-85

Mitchell B 1971 The weights of new-born one-day-old red deer calves in Scottish moorland habitats. *Notes from the Mammal Society 164:* 250-254

Mitchell B and McCowan D 1986 Performance and Population Dynamics in relation to Management of Red Deer (*Cervus elaphus*) at Glenfeshie, Inverness-shire, Scotland. *Biological Conservation 37:* 237-267

Mitchell B, Staines B W and Welch D 1977 *Ecology of Red Deer. A Research Review Relevant to their Management.* Institute of Terrestrial Ecology: Cambridge, UK

Nelson M E and Mech D 1981 Deer social organization and wolf predation in northeastern Minnesota. *Wildlife Monographs 77*: 1-53

Pollard J C, Littlejohn R P and Suttie J M 1992 Behaviour and weight change of red deer calves during different weaning procedures. *Applied Animal Behavioural Science 35*: 23-33

Pollard J C, Littlejohn R P and Suttie J M 1993 Effects of isolation and mixing of social groups on heart rate and behaviour of red deer stags. *Applied Animal Behavioural Science 38:* 311-322

Putman R J 1988 *The Natural History of Deer.* Christopher Helm: Bromley, UK

Ratcliffe P R 1984 Population dynamics of red deer (*Cervus elaphus* L.) in Scottish commercial forests. *Proceedings of the Royal Society of Edinburgh 82B:* 303-319

Schwede G, Hendrichs H and McShea W 1993 Social and spatial organization of female white-tailed deer, *Odocoileus virginianus,* during the fawning season. *Animal Behaviour 45:* 1007-1017

Shackleton D M and Haywood J 1985 Early mother-young interactions in California bighorn sheep, *Ovis canadensis californiana. Canadian Journal of Zoology 63*: 868-875

Sibbald A M, Fenn P D, Kerr W G, Loudon A S I 1993 The influence of birth date on the development of seasonal cycles in red deer hinds (*Cervus elaphus). Journal of Zoology 230: 593-607*

Smith P S 1987 Maternal defense in Columbian white-tailed deer: when is it worth it ? *The American Naturalist 130 (2):* 310-315

Sokal R R and Rohlf F J 1981 *Biometry, 3rd edition.* W H Freeman: Oxford, UK

Suttie J M 1983 Body size: dominance relationships in red deer stag calves. *Animal Behaviour 31:* 610-611

Thouless C R and Guinness F E 1986 Conflict between red deer hinds: the winner always wins. *Animal Behaviour 34:* 1166-1171

Trivers R 1985 *Social Evolution.* Benjamin-Cummings: Menlo Park, USA

Whitehead G K 1964 *The Deer of Great Britain and Ireland, an Account of their History, Status and Distribution.* Routledge and Kegan Paul: London, UK

Yahner R H 1980 Barking in a primitive ungulate, *Muntiacus reevesi:* function and adaptiveness. *The American Naturalist 116:* 157-177

Yerex D and Spiers I 1990 *Modern Deer Farm Management.* GP Books: Wellington, New Zealand

Youngson R W 1970 Rearing red deer calves in captivity. *Journal of Wildlife Management 34:* 467-470