MATING STRATEGIES OF JAPANESE SIKA DEER (*Cervus nippon nippon*) ON LUNDY

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SUMMARY

While previously considered to be a territorial species, Sika deer have displayed adaptability in their mating systems in a wide range of habitats. This study focused on the population of approximately 35-45 Japanese Sika deer (*Cervus nippon nippon*) occupying the south-eastern sidelands of Lundy. Intensive observations were carried out over the 12th-30th October 1996 which includes the rutting season, during which 10 stags were identified and grouped into three separate age classes. Stag home-ranges suggested that the Lundy Sika were not territorial but demonstrated a roving strategy, whereby males mated with oestrus females as they encountered them. A dominance matrix of stag fighting success emphasized the presence of an age-related dominance hierarchy which was reflected in the sexual interactions between the males and the females. Various factors affecting the Lundy Sika were assessed concluding that poor habitat resources and intense overcrowding had produced the unusual behaviour patterns observed.

INTRODUCTION

Mammalian mating systems are dependent upon the extent to which the reproductive rates of females can be increased by male parental investment and consequently how many offspring a single male can effectively produce (Clutton-Brock 1989; Emlen and Oring 1977). They can be monogamous, polygamous, polyandrous, polyganous or promiscuous, with the costs of rearing offspring being an important factor.

Cervid species are habitually polyganous and investigations have described the predominating strategy as harem-defence (Clutton-Brock *et al.* 1989), although certain species exhibit resource-defence and lek-breeding strategies (Apollonio *et al.* 1990). The causes of these variations are the spatial distribution of resource habitats and consequently, the social behaviours of females. It has been shown that alterations in these ecological conditions, such as concentrations of females around resource patches (Alvarez *et al.*1990) or experimentally determined resource availability (Carranza *et al.* 1990,1995; Carranza 1995), can lead to a shift towards a more cost-efficient mating pattern within a particular population.

One of the most flexible examples of such adaptability is seen in the density-related mating strategies of Sika deer. While Sika demonstrate habitual defence of territories in their native Japanese islands (Miura 1984), elsewhere they have been seen to switch from lekking behaviour to forming dispersed rutting stands due to a decline in numbers rather than an alteration in other ecological variables (Balmford *et al.*1993).

The population of Japanese Sika deer on Lundy were introduced in 1927 along with Fallow and Red deer (Linn 1997, 113-4; Bath and Scriven 1975). Of the three species, the Sika seem to have adapted best to the island habitat and conditions, their numbers increasing

as the Fallow and Red eventually died out. Little is known about the rutting habits of the Lundy Sika. In their study of Sika deer in the British Isles, Horwood and Masters (1981) referred to the Lundy population as equivalent to a park herd due to the small, managed numbers. Since 1973, however, there have been no cullings and consequently, the population has been left to manage itself. This study has focused upon this herd as a previously unstudied example of introduced Sika in an environment that is constrained by size, habitat diversity, resources and carrying capacity.

In his extensive study of Sika in Japan, Miura (1984) demonstrated the existence of territoriality on the basis of behavioural characteristics exhibited by males and the spatial distribution of their home-ranges. By identifying three basic categories of behaviour patterns - dominant, contact and submissive - territorial males could be distinguished from non-territorial and the subsequent stag hierarchy used to predict copulatory success. Home-ranges of territorial males did not overlap significantly, unlike those of non-territorial males, and certain behaviours and marking patterns denoted particular territories within these ranges.

This investigation aimed to examine the behaviours of the Lundy Sika during the October rut. By analysing the interactions between males it was hoped that a hierarchy of social rank could be established amongst the stags which could then be used to interpret the particular mating behaviours occurring. Using information regarding the topography, area and vegetation of the Sika range, the general movements of the herd could be identified. The study then attempted to establish whether a territorial mating strategy occurred and if not, how the immediate social, ecological and population dynamics had combined to select the particular competitive strategy displayed.

METHOD
Study Site
This is an area of approximately 0.6 kms² stretching 1.86 km along the east side from Ladies Beach northwards to Knight Templar Rock, encompassing the area in which the Sika are most active. The site is bounded to the west by the main track up the island and by the cliffs to the east. Millcombe valley provides the southern perimeter and the most northerly sightings of deer formed the enclosing boundary. Deer were sighted outside these areas although this was infrequent and only temporary.

Introduced rhododendron (*Rhododendron ponticum*) forms several dense thickets that provide shelter and protection for the deer and strongly influence their ranges. Four main thickets exist in the lower half of the site, outlining the steep sides of the gullies. These thickets are smaller and more dispersed from Quarter Wall northwards up to the Halfway Wall slopes. Since 1986 several thickets beyond Threequarter Wall have been cleared (National Trust 1986). *Calluna* heather bushes dominate the grassland on top of the island beyond Quarter Wall whilst Tillage and Brick Fields are enclosures of improved grass. Along the length of the sidelands the amount of cover accessible is inversely proportional to the quality and availability of the vegetation. When recording the location of interactions, the study site was therefore divided up into zones defined by different habitats or spatial boundaries.

Lundy Sika Deer
An estimate in 1975, two years after the last cull, placed the population size at 30 individuals, nine stags and 21 hinds and juveniles (Bathe and Scriven 1975). A population analysis of the herd in April 1996 based on sightings reported 33 distinct individuals made up of nine

stags, 18 females and six juveniles (Thomas 1996) suggesting a total population of between 35-45.

Procedure

An intensive observational study was carried out from 12th-30th October 1996. Observational times were roughly between 06.30 and 11.30 hrs and between 15.00 and 19.00 hrs to approximately coincide with the diurnal patterns of the deer. The ten stags were classified into three main age-groups according to their antler configurations (Miura 1984; Horwood and Masters 1981). Age Class I members were classified as between 1-2 years and included three prickets; Age Class II were stags aged between 3-5 years and comprised four 6-points; Age Class III described stags over five years and contained an unusually well-developed 6-point stag and two 8-points (see Fig 1.)

The topography of the study area made it impossible to observe more than one habitat zone at a time, so observational methods were carefully structured to include both stationary observations and tracking. Depending on the time of day and the direction of the wind, the particular areas favoured by the deer were examined in turn until deer were sighted. All interactions between deer were observed through binoculars and recorded into a dictaphone or notebook for later entry into a computer.

In order to establish home-ranges and any existence of territories, the exact location zone of all stag sightings was recorded along with time of day, group size, all other stags present, and any interactions occurring. Aggregations of deer in one habitat type were considered as a single group if they were browsing on the same slope or gully, unless close associations of deer moving together made a separate grouping necessary.

Male-male interactions were divided up into confrontations between two individuals and those that involved more than two individuals; the latter were recorded as sets of dyadic interactions. Using as a model the classification of interaction patterns identified by Miura (1984), 12 self-explanatory behaviour patterns were recorded in three categories as follows (see Thomas 1997):

Dominant:	Aggressive Approach, Nose-up Display, Chasing
Contact:	Sniffing/Muzzling, Lateral Display, Low Presentation of Antlers,
	Touching Antlers, Sparring, Provocation, Clash
Submissive:	Walk Off, Run Off

Similarly, male-female interactions were classified into the following phases:

| Preliminary:	Sexual Approach, Low Stretch, Following
Enclosing:	Nose-up display, Chasing
Mount:	Mount, Copulation

As marking patterns and vocalizations are equally important in determining territoriality, the nature and location of all such behaviours were recorded with the age class of stag. Vocalizations included loud roars and high pitched moans, usually a groan starting extremely
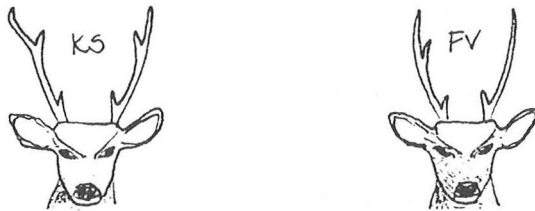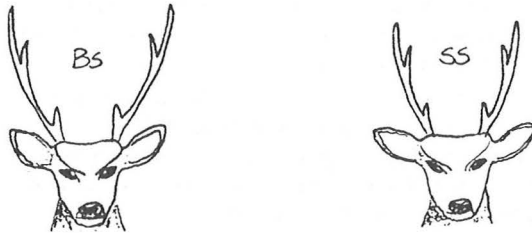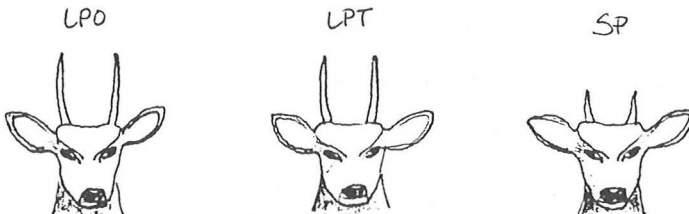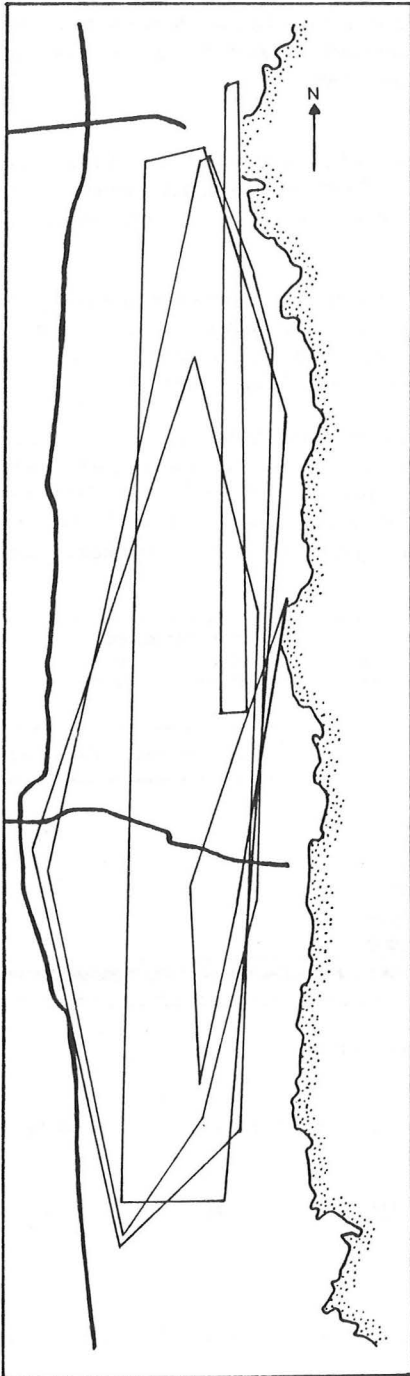
Figure 1.

SCALE

0   300 M

Figure 2: Convex polygons showing the home-ranges of five dominant stags. The area shown is the East Sidelands from Halfway Wall in the north to Tillage Field in the south.

high and then descending to a louder roar, but not alarm whistles or barks, made by both males and females. Marking patterns were identified as thrashing vegetation with antlers, pawing and rubbing facial scent glands against trees.

RESULTS
In total, 63 separate sightings were made, within which 22 male-male interactions and 41 male-female interactions were observed. Of the males-female interactions, three complete copulations were recorded, two by the large 8-point *BE,* and the other by the small 6-point *SS*

Spatial Distributions
Home-ranges were investigated by plotting the sightings and interactions of individual males on to a map of the study site. Minimum convex polygons were then constructed by connecting the outermost points to give a diagrammatic view of each stag's range. These overlap considerably, several stags sharing almost identical ranges (Fig. 2).

Fig.3 demonstrates that the majority of both male-male and male-female interactions were concentrated in Quarter Wall Gully. Subsequent to this, the remaining interactions seem to be distributed across all areas with the exception of Northern Gully and Brick Field. The distribution of interactions does not correlate with the outer limits of the home-range polygons, as might be expected from boundary defence, but is visibly concentrated towards the centre of the range shared by several stags.
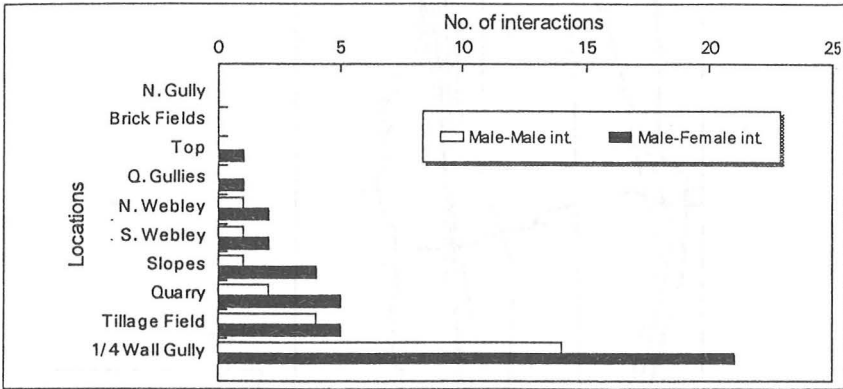

Figure 3. Number of interactions per location.

Interaction Patterns
The number of dominant and submissive behaviours displayed by each age class are as follows:

AGE CLASS	III	II	I
Dominance patterns	8	7	1
Submissive patterns	1	6	4

Although the frequencies are too small to compare with expected observations, a slight

trend appears towards age-related dominance. Although only marginally so, the number of dominance patterns performed was proportional to the age class of the performer, and the frequency of submissive patterns was inversely proportional, as would be expected.

To investigate this putative trend further, Table 1 shows a dominance matrix constructed by plotting the frequency with which each male 'won' against each individual contested. The matrix was organised by age class and according to the number of antler points within classes.

		BE	SV	WG	BS	KS	SS	FV	LPO	LPT	SP
L	BE										
	SV	1									
O	WG										
S	BS	1	1								
E	KS										
R	SS	1	1			1	1				
	FV		1					1			
	LPO							1			
	LPT										
	SP	1	1	1			1				

Table 1: Dominance matrix to show number of interactions won by individuals.

The matrix highlights a relatively stable positive correlation between age class and dominance. Older stags consistently beat younger stags and, within age classes, stags with more antler points overpowered those with fewer, signifying a clear linear dominance hierarchy. An obvious exception is the individual *WG*. The distortion apparent in the matrix here is due to the relative infrequency of sightings for this particular stag.

If the social status of the males postulated by the matrix is accurate, an age-ranked dominance should be apparent in the male-female interactions observed. The distribution of the interactions between age class is as follows:

AGE CLASS	III	II	I
INTERACTIONS	21	16	14

A chi-squared test was carried out testing the null hypothesis that interactions with females should occur with the same frequency irrespective of age and social class. The discrepancy between observed and expected frequencies was found to be significant at the 1% level (chi-square = 11.76 $p<0.01$ d.f.=2) supporting the findings from the dominance matrix.

As defined in the Procedure, male-female interactions were divided into three distinct phases: preliminary, enclosing and mount. Figure 4 compares the numbers of behaviour patterns within each phase for each age class in turn to see which phases, if any, are characteris-
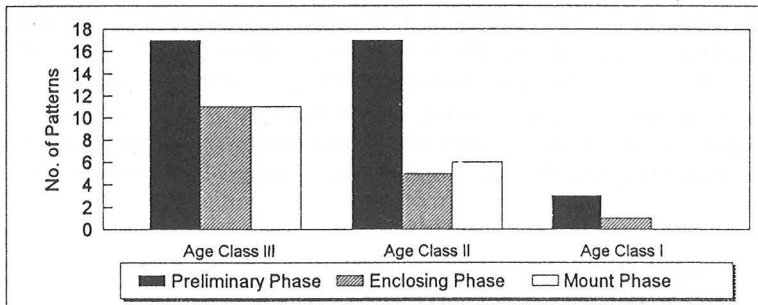
Figure 4: Frequency of behaviour patterns within interactions.

tic to which social status of stag. The most prevalent phase of the three is the preliminary, with both age classes III & II demonstrating equal frequencies of behaviours. Subsequently, the following phases are significantly reduced and biased towards age class III stags. The drastic reduction in behaviour patterns from the preliminary to the enclosing and mount phases in age class II particularly, indicate that whilst all stags of age classes III and II perform sexual approaches towards females, those stags belonging to a higher social class and age bracket are more successful.

Marking Behaviours and Vocalizations

In addition to analysis of the sexual interactions observed, Figure 5 shows which stags performed several vocalizations and distinctive territorial marking patterns. The majority of marking behaviours and all vocalizations were displayed by the stags in age class III, and the distributions of the former show a defined association between frequency and dominance. Although both behaviours occurred infrequently the findings strongly imply a social dominance ranking in accordance with age class.
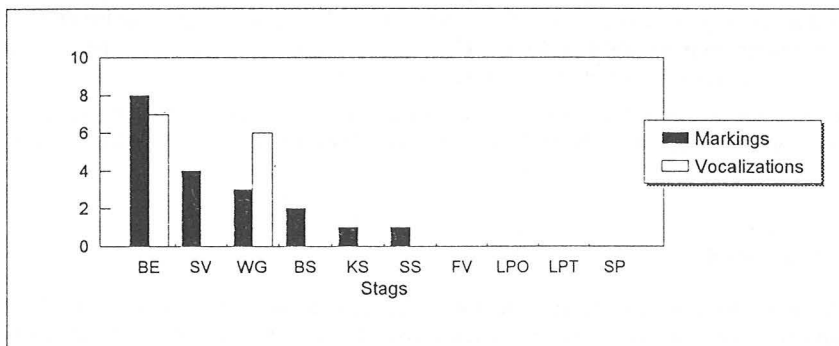

Figure 5: Frequency of marking behaviour and vocalization within each age class.

Habitat Utilization

Within a population, habitat utilization can yield explanations of the social and reproductive behaviours of the individuals. Between populations, variations in such conditions can reflect

the direct effects of particular environments upon their inhabitants. A measure of such utilization can be gauged by the size of deer groups in different habitats within the study site, bearing in mind that group size and composition changes dramatically during the rut where sexual segregation is abandoned.

Although the study site is divided up into individual areas, these can be collapsed into five characteristic habitat types. Numbers of individuals in all groups observed were recorded and the mean group sizes for each of the five areas was calculated. The results were as follows:

AREAS	Slopes	Fields	Top	Gullies	Quarry
MEAN	9.0	6.7	5.0	3.9	3.2

Differences between the group sizes were tested using analysis of variance, and were found to differ significantly depending upon the habitat ($F=4.62$, $p<0.002$ d.f.= 4).

DISCUSSION

Evidence supporting territoriality on Lundy is extremely weak. The almost identical home ranges of the stags demonstrates a distinct lack of spatial boundaries crucial to territoriality. The repertoire of the particular marking behaviours used to emphasize these boundaries also seems to be restricted in the Lundy Sika. Other investigations have reported severe tree-bole damage, large areas of thrashed *Calluna* bushes (Putman 1986, Horwood and Masters 1981), rubbing, pawing and urination (Miura 1984). Of the very few marking patterns observed in this study, none involved bole-marking, rubbing or urination. In accordance with Miura's findings (*ibid.*), the majority of marking patterns were carried out by age class III males but they did not coincide with the defence of territories. Eleven of the 14 observations occurred in the same area and involved four males, emphasizing the acknowledged overlap in ranges. This presents spatial and behavioural evidence strong enough to dispel any suggestion of territoriality.

It is clear that there is a concentration of activity within Quarter Wall Gully. This forms the focus for the majority of male-male interactions, male-female interactions, and marking behaviours, implying a significant designated area that suggests an alternative resource-defence strategy. Lek-breeding strategies have been reported for Sika (Balmford *et al.* 1993), but the characteristic behaviours are much less flexible than those identified on Lundy. Lekking implies a distinct area in which all the potential breeding males are involved in the highly aggressive defence of clustered territories (Festa-Bianchet *et al.*1990; Clutton-Brock *et al.*1993) along routes of high female traffic, or 'hotspots' (Bradbury *et al.* 1986). The occurrence of sexual interactions by many males elsewhere in the study site, and the low level of aggressive interactions between males, suggests that this is not the case. Lekking also requires female mate choice at the lek site, a characteristic absent in the Lundy Sika. Despite its focus of activity, Quarter Wall Gully did not form a female congregation area. More males were observed in the gully than females, which would produce an inadequate site for male displays. Males often chased or followed females across the entire gully, initiating few aggressive responses which might be expected from a lek.

Across all areas, the proportion of male-female interactions is consistently higher than aggressive interactions between male dyads, suggesting that resource-defence has been replaced by the defence of females. Harem-defence as a strategy, however, does not reflect either the male-female behaviour patterns observed or the relatively static congregations of

individuals in Quarter Wall Gully. Harem-gathering suggests high mobility amongst both males and females as well as unimale dominance of large female groups; neither situation is apparent in the Lundy Sika.

The reproductive behaviour closest to that observed on the study site seems to be what is described as the roving strategy (Owen-Smith 1977). This pattern has been recorded in New Forest Sika (Putman 1986; Putman and Mann 1990) where males either patrol areas of high quality resources and mate with oestrus hinds when they encounter them, or where males specifically forage for individual oestrus hinds by covering areas of high hind density. The Lundy Sika seem to use a strategy whereby males share a similar range to that of the females, travelling between the differing resource areas and covering oestrus females when they find them or when their routes are intercepted.

Habitat Distribution

The distribution and quality of available habitats has a direct effect upon the possible energy-intake levels of the individuals. The study site is characterized by the relatively homogenous sidelands where grazing is of poor nutritional quality, bordered by large open areas of superior foraging quality. Such a situation does not favour the establishment of territories, as all males would be defending similar areas of poor quality resources and the areas of valuable resources worth defending would be too costly on Lundy due to lack of shelter.

The severe lack of tree cover across the range of the study site could present several ecological problems for the Sika. Typically, Sika deer inhabit thick coniferous forests used as both shelter and food. Evidence from Roe deer populations (Loudon 1982) has shown that body weight, and therefore ovulation rate, is governed by the specific forest habitat type, emphasizing the importance of the forest for the Roe ecology. The absence of any forest habitat in the Lundy study site may well prove to be a strong influencing factor upon the mating strategy.

Population Density

Despite the fact that group size increases as a function of open habitats and the rut, the mean group sizes of the Lundy Sika are considerably larger than those commonly reported, even those in unusual circumstances. Larger group sizes can range from between about 5-11 deer and the largest recorded group reached 12 individuals (Putman 1986). This is challenged by the Lundy population where groups can number up to 15 outside the rutting season (Thomas 1996), and during the study period where groups regularly contained between 10-15 deer in Tillage Field after dark. In the absence of tree cover, the shelter provided by the rhododendron thickets may be so crucial to the Sika ecology that the population will risk severe overcrowding to remain close to these existing plantations.

The population density with regard to the carrying capacity of the study site is almost definitely a contributing factor to the unusual social organization. As recorded, the approximate density of the Sika population is >30 deer/km². This dramatically exceeds the estimate for a high density Roe deer population of >20 deer/km². Within the Roe population, an increase in density directly altered the breeding sex ratio in favour of females and reduced the mean territory sizes of the males (Loudon 1982). It seems possible, therefore, that territoriality is prevented in the Lundy Sika by the unusually small size of the habitat.

Changes in male reproductive rates can also be caused by increased population density and limitation of resources. These factors lead to a subsequent intensification of male competition

petition which can result in the costs of resource defence becoming too high and a territorial strategy being abandoned in favour of direct male-male competition (Emlen and Oring 1977). This increase in competition also affects the dominance rankings, requiring the social hierarchy to be frequently contested. This seems to have been the case on Lundy where a dominance hierarchy has been established in preference to the high cost of resource-based defence.

ACKNOWLEDGMENTS

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