

## VARIATION OF MATING SYSTEMS OF INTRODUCED SIKA DEER

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Sika deer (*Cervus nippon*) exhibit an unusual degree of variability in their mating system. Direct harem defence has been recorded in New Zealand (Kiddie, 1962) and England (Putman & Mann, 1990). While, resource-based territories have been reported for native sika in Russia (Yevtushevskiy, 1974) and Japan (Miura, 1984), and for introduced populations in England (Horwood & Masters, 1970) and Ireland (Gradl-Grams, 1982). In the Czech Republic, we observed lek territoriality in Sika in the Manětín Forest, Western Bohemia (Bartoš *et al.*, (1991). This elicited our attention to this population for a further four seasons (see also Balmford *et al.*, 1993). The only other deer species known to exhibit a comparable flexibility of mating system appears to be the Fallow deer (*Dama dama*, Langbein & Thirgood, 1989), and possibly the Red deer (*Cervus elaphus*, Carranza *et al.*, 1990; Carranza, 1992; Pereladova, pers. comm.).

This paper analyses mating systems according to classification by Langbein & Thirgood (1989) and summarizes records of Sika rutting behaviour at Manětín over five seasons from 1989 to 1993. To make it complete, we have also used extracts from two previously published reports (Bartoš *et al.*, 1991; Balmford *et al.*, 1993).

## METHODS

Sika were studied from 1989 to 1993 in a ca 20 km<sup>2</sup> section of the 220 km<sup>2</sup> Manětín Forest. Vegetation consisted of a mixture of open pasture (43 %) and commercial forests (spruce 53 %, pine 40 %, and other tree species 7 %). Sika at Manětín are strictly nocturnal as a result of hunting pressure, disturbance by tourists, and people gathering mushrooms during the daylight hours. We, therefore, monitored rutting activity by recording the direction of male calling from twelve different sites (Bartoš *et al.*, 1991; Balmford *et al.*, 1993). These sites were distributed attempting to cover the whole area. Male calling was heard exclusively after sunset. Observations in 1990 (Balmford *et al.*, 1993) demonstrated, that

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calling peaked at about 2200 hours and declining remarkably after midnight. We listened from four or more of these sites between 1900 and 2200 hours for one day (1991), two days (1989, 1992), or three days (1993) at the usual peak of the rut (14th to 16th October). Local foresters suggested the date of observations as they were able to estimate the approach of the peak of the rut. In 1990 recording lasted three weeks (Balmford *et al.*, 1993), however, only data for the analogous three days of 1990 are used in this study. In each year, we were able to cover most of the study area. We recorded the time and direction of each male calling bout, each bout consisting of one to four calls (Miura, 1984). When calling bouts were heard simultaneously, from more than one monitoring site, the locations of calling males were determined by triangulation. Such locations are referred to as 'sites'. If calling bouts were only heard from a single monitoring site, they were omitted from this study. From 1991 onwards we counted Sika in open areas using a spot light from a car, both before (approximately between 1800 and 1900 hours) and after (approximately between 2200 and 2300 hours) recording sessions. However, it was not usually possible to visually determine the number of males at each site.

We classified the observed activities according to definitions given by Langbein & Thirgood (1989). Territorial activities were regarded in the three following categories:

- 'Stand' — A single mature male defends an exclusive reproductive territory. Stands may vary greatly in habitat type and in size and may be clumped or widely dispersed.
- 'Temporary stand' — A similar strategy to the above but one in which the stand is only defended for a relatively small proportion of the day.
- 'Lek' — range in composition from 5 to 25 mature males, characterized by a reduction of individual territory size to as little as  $5 \times 5$  m.

According to these definitions we have formulated presumptions for individual categories (Table I) and applied them to the data collected. With a limited possibility to observe the mating activity visually, temporary stands appear difficult to distinguish from non-territorial strategies.

TABLE I

*Presumptions for individual categories of territorial strategies.*

Activity	Stand	Temporary stand or non-territorial strategies	Lek
Calling sites widely dispersed over the area	Yes/No	No	No
Calling activity reduced to a small proportion of the day	No	Yes	Yes
Females in proximity to calling males	Yes/No	Yes	Yes
Repeated calling activity in the same site in successive days	Yes	Yes/No	Yes/No
Local calling frequency higher than in other sites	No	No	Yes
Reduction of the distance between calling males to only a few metres	No	No	Yes

If not stated otherwise, the data were analysed according to the General Linear Models Procedure (GLM) for Unbalanced ANOVA (SAS). The classes used were 'Calling frequency of the site' ('A site with the highest calling frequency' and 'Other sites') and 'Season' (1989 to 1993). Least-squares means (LSMEAN) were computed for each class and differences between classes were tested using a t-test.

## RESULTS

### DISTRIBUTION OF CALLING SITES

The distribution of locations for calling males, over the years studied, is shown in Fig. 1. In each monitored season, calling activity was unequally distributed over the area, usually concentrated in fields near the forest surrounding the small village of Lipí. The maps in Fig. 1 show ca 20 % of the area covered by the observers; there were no records of Sika calling in the rest of the area (mostly forested habitat).

### PROXIMITY OF FEMALES TO CALLING MALES

The results of observations of deer seen during the spot light searches are shown in Fig. 2. We could only compare the locations of calling activity with visual records of deer numbers when the calling locations were outside the forest and hence visible from a car. In all 10 instances where such a comparison was possible, calling activity coincided with the presence of deer of both sexes (Sign test,  $P < 0.001$ ). No significant relationship was found between calling frequency and the number of deer present at these sites (Spearman rank correlation  $r_s = 0.41$ ,  $n = 10$ , NS).

### REPETITION OF CALLING IN SAME SITES ACROSS SEASONS AND IN SUCCESSIVE DAYS

When possible we compared calling on successive nights to establish whether sites were consistently occupied. Calls were heard from the same site on consecutive nights in 67 % (1989,  $n = 3$  sites), 47 % (1990,  $n = 17$  sites), 25 % (1992,  $n = 8$  sites), and 64 % (1993,  $n = 14$  sites) of the cases. Across all seasons, only 50 % of sites were occupied on successive nights. This suggests that the sites do not necessarily represent permanent territories.

### DIFFERENCES IN CALLING FREQUENCIES BETWEEN SITES WITHIN AND ACROSS SEASONS

We calculated frequency of Sika male calling bouts, by hour, for all sites daily. In all seasons, certain sites showed a higher calling frequency than the other sites. Proportions of all calling bouts within the session at these most active sites were 92.16 % (1989), 77.17 % (1990), 50.67 % (1991), 56.88 % (1992), and

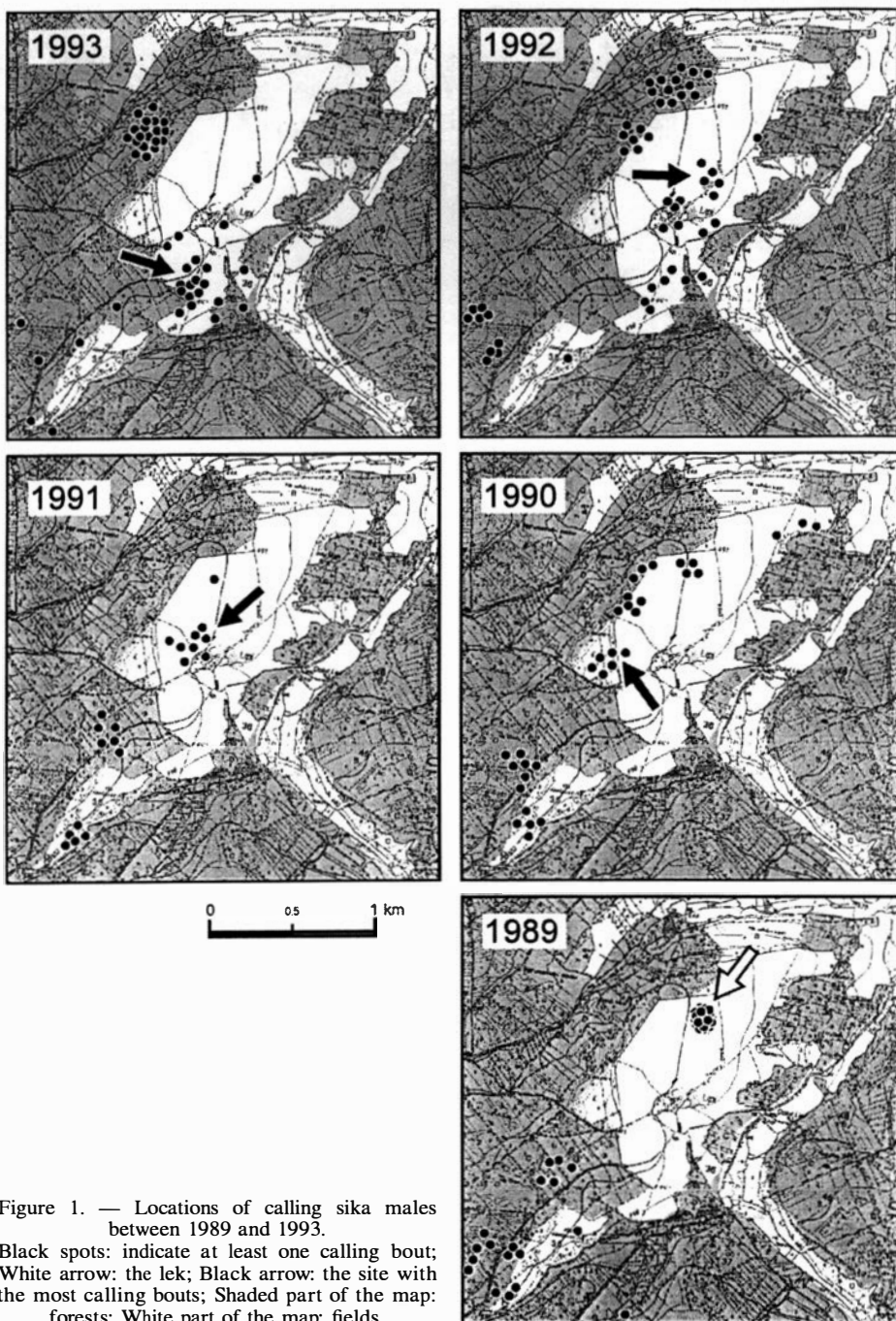


Figure 1. — Locations of calling sika males between 1989 and 1993. Black spots: indicate at least one calling bout; White arrow: the lek; Black arrow: the site with the most calling bouts; Shaded part of the map: forests; White part of the map: fields.

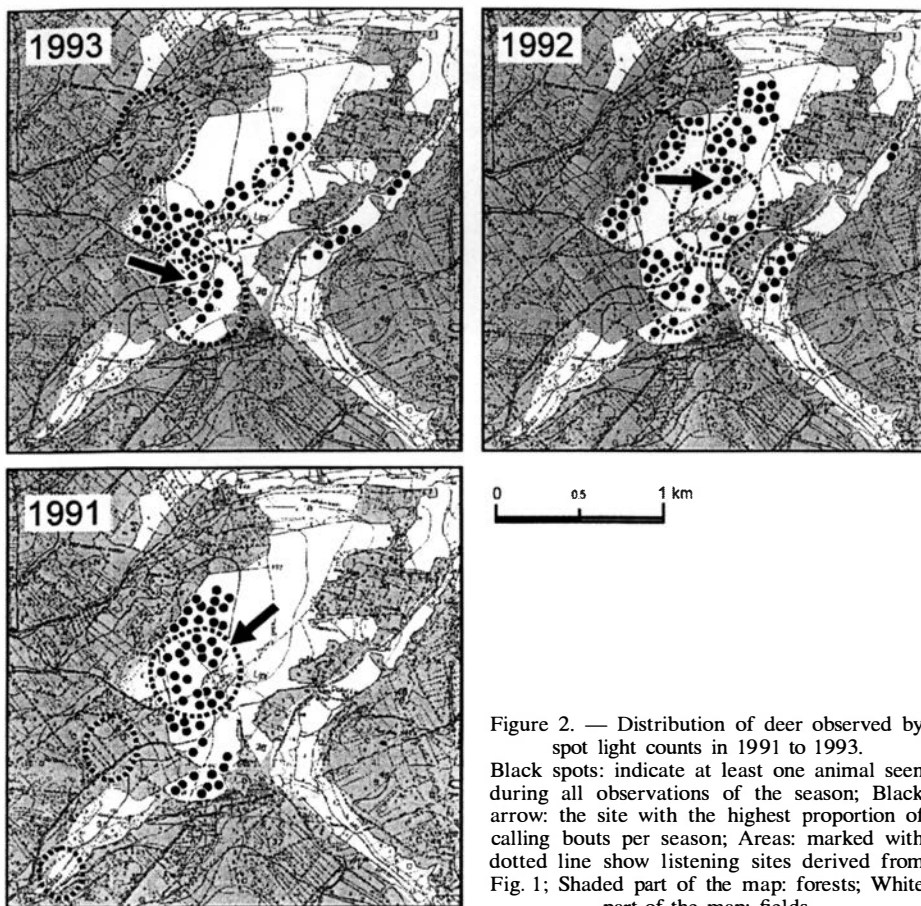


Figure 2. — Distribution of deer observed by spot light counts in 1991 to 1993. Black spots: indicate at least one animal seen during all observations of the season; Black arrow: the site with the highest proportion of calling bouts per season; Areas: marked with dotted line show listening sites derived from Fig. 1; Shaded part of the map: forests; White part of the map: fields.

58.75 % (1993). For statistical analysis, data from all seasons were combined and subjected to GLM. Calculation was carried out in two steps.

First, we compared seasons. The GLM model containing the only class 'Season' showed significant variation in calling frequency between seasons (inserted part in Fig. 3,  $F_{5,41} = 4.83$ ,  $P < 0.01$ ). Calling frequency in 1989 was higher than in 1990 ( $P < 0.05$ ), 1992 ( $P = 0.07$ ), and 1993 ( $P = 0.06$ ), but not in 1991 ( $P = 0.1671$ ). The calling frequencies in all other seasons did not significantly differ from each other.

Second, we compared hourly calling frequencies between the sites with the highest calling activity and the other sites (Fig. 3). For this, the class 'Calling frequency of the site' was nested within 'Season'. There was a significant variance between sites and seasons ( $F_{9,41} = 15.40$ ,  $P < 0.001$ ). Only in 1989 did the site with the highest calling frequency produce significantly more calling than the other sites ( $P < 0.005$ ).

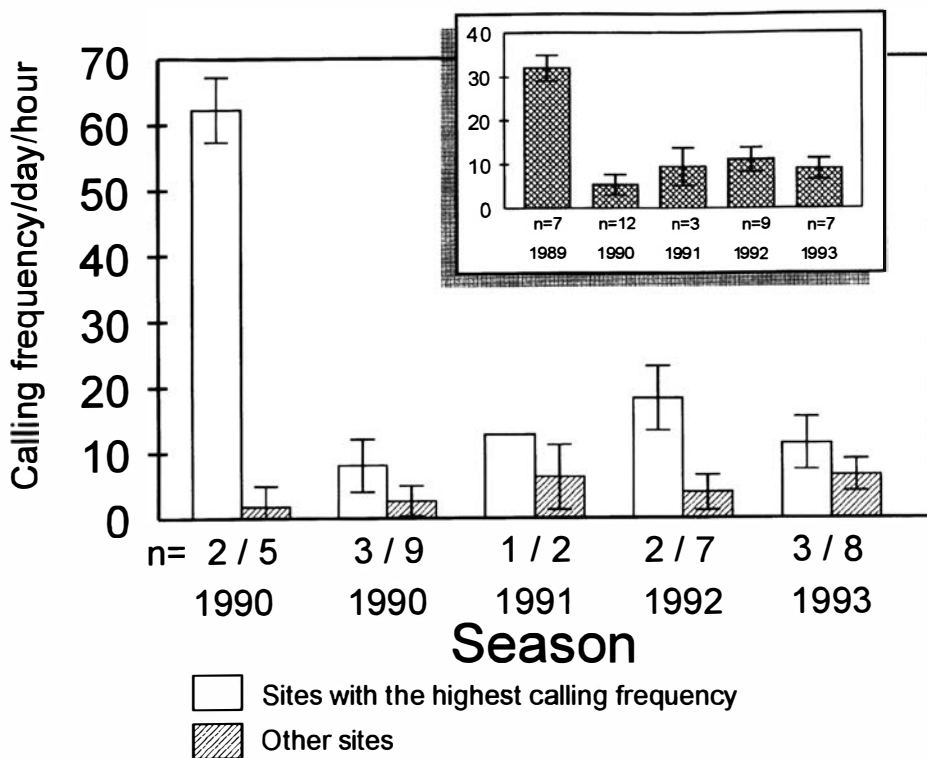


Figure 3. — The mean hourly frequency (LSMEAN  $\pm$  S.E.) of Sika male calling bouts per site per day, and sites with the highest proportion of the records across seasons. Inserted part shows calling frequency (LSMEAN  $\pm$  S.E.) between seasons. Black bars: Calling bouts per site per day; White bars: Calling bouts per site with the highest activity per day.

It is interesting to note that since 1991, calling was frequently heard in village gardens within tens of metres of the houses. In 1991 this site had even the highest calling activity (Fig. 1, middle left).

#### THE DISTANCE BETWEEN CALLING MALES

In 1989 the shortest distance between calling males was approximately 40 m on a putative lek, when up to 7 males were rutting on a spot of about 300 m in diameter (Bartoš *et al.*, 1991). In all other seasons the inter-male distance did not fall below several hundred metres.

During daylight we examined calling sites in order to quantify pawing or scraping activity, as a possible sign of territorial behaviour. Although in 1989, the lek did contain clusters of scrapes (*ibid.*), in other seasons we found as many scrapes at other sites as at calling sites.

## DISCUSSION

In the studied population of Sika deer, the mating system has evidently changed across seasons. A typical resource-based territorial system, as described in most native or introduced Sika populations (Horwood & Masters, 1970; Yevtushevskiy, 1974; Gradl-Grams, 1982; Miura, 1984), appears unlikely in the Manětín Forest. Although conditions for true lekking (Table I) were fulfilled only for observation in 1989 (Bartoš *et al.*, 1991), from 1990 to 1993 calling males were also aggregated, and in each mating season the distance between extreme calling positions did not usually exceed 2 km. In contrast to true lekking behaviour, however, rutting stands in these later years were usually located on or close to resources used by females.

Where we could monitor deer both visually and acoustically, we usually found that calling sites were located in areas with concentrations of deer (Fig. 2). These sites were not necessarily in the same place on consecutive nights. Instead, it seemed that calling males moved into areas where the hinds had relocated. This may explain why we failed to find any consistent relationship between scrape location and calling activity. In some other species scraping is facultative and not necessarily linked to territory marking (Hirth, 1977). In White-tailed deer, scraping serves as a means of communication between bucks and does during the breeding season (Kile & Marchinton, 1977; Miller *et al.*, 1987; Ozoga, 1989), with most scrapes being made by mature, dominant, males to intimidate rival males and to attract breeding females (Marchinton & Hirth, 1984). Marchinton & Atkeson (1985) suggested that territoriality in White-tailed deer is facultative, and depends on resource distribution and population demography. This facultative interpretation of territoriality may also explain its absence in Sika deer in Manětín, where permanent harassment by humans during daylight prevents the males from establishing themselves in fixed locations (Bartoš *et al.*, 1991).

We conclude that Sika males in Manětín occupy temporary rutting stands located in open pasture, mature forest, and in the boundaries between these two habitats. Males also called extensively from within the village gardens. These stands do not seem to be permanent resource-based territories held throughout the mating season (reported Yevtushevskiy, 1974 and Miura, 1984). Instead, the stands are clustered, temporarily, in areas where resources used by females are particularly concentrated, or on paths used by females commuting between resources. This gives the deer advantages similar to those arising through lekking; females benefit from increased opportunity to choose a mating partner quickly, they are able to compare males closely and also have the possibility to monitor choices of other females (Bradbury & Gibson, 1983; Clutton-Brock *et al.*, 1988; Clutton-Brock *et al.*, 1989). Nevertheless, it is apparent that because the males are more dispersed, the opportunities for females to assess and compare them are less than on a lek. True lekking in Sika seems to occur only in high density populations (Bartoš *et al.*, 1991; Balmford *et al.*, 1993). Sika thus prove to be successful opportunists that can adapt flexibly to changing environments.

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## SUMMARY

The mating system of feral Sika deer (*Cervus nippon*) in the Manětín Forest (220 km<sup>2</sup>), Czech Republic, was studied from 1989 to 1993. The Sika were strictly nocturnal due to hunting pressure and continuous human harassment during daylight. We therefore monitored rutting activity by triangulating male Sika calls recorded from different sites, and also by counting Sika in open areas using a spot light. In all seasons, calling activity was unequally distributed over the area, usually concentrated in fields close to the forest. In 1989 the Sika established a lek. Later, the mating system changed to dispersed rutting stands. These rutting stands were occupied intermittently and were located in open pasture, mature forest, and in the boundaries between these two habitat types.

## RÉSUMÉ

Le système d'appariement de Cerfs Sika (*Cervus nippon*) introduits dans la forêt de Manetin (220 km<sup>2</sup>), République tchèque, a été étudié de 1989 à 1993. Le Sika était strictement nocturne en raison des pressions de chasse et des dérangements continus par l'homme dans la journée. Les activités de rut ont été suivies par triangulation des cris des mâles en divers sites, ainsi que par comptage au phare des cerfs dans les zones ouvertes. Durant toutes les saisons, les activités vocales ne furent pas réparties uniformément sur la zone d'étude, étant généralement concentrées dans des champs proches de la forêt. En 1989, un lek fut constitué. Par la suite, il éclata en arènes dispersées. Ces arènes furent occupées par intermittence et étaient localisées tant dans les pâturages ouverts qu'en forêt mature et à l'interface de ces deux types d'habitat.

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