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The effect of female distribution on male territoriality in Chinese Water deer (*Hydropotes inermis*)

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Abstract

Territoriality in the Chinese water deer (*Hydropotes inermis*) was studied in its native habitat at Poyang Lake, Jiangxi, China. Adult males held small territories of 0.5 ha on average during the mating season. The territorial grounds were located according to the ranging behavior of females. Males held clustered or individual mating territories in areas frequented by females. Male territoriality showed daily fluctuation following the change in female density within males' territories. Our findings provide strong evidence that male spatial behaviour in the mating season is primarily determined by female distribution pattern in the water deer.

Introduction

In species lacking male parental care, such as ungulates, males are selected to increase their reproductive success through increasing copulations (Clutton-Brock et al. 1982). Since the distribution patterns of receptive females construct the spatial feature of mating opportunities, mating tactics of males are determined, directly or indirectly, by female distributions (e.g., Jarman 1974; Parker 1978; Bradbury 1981; Gosling 1986; Rubenstein 1986). Therefore, the diversity and dynamics of female distribution may impose a strong effect on the form and fluctuation of male spatial behaviour. The intra- and inter-specific variations in the distribution of cervid females could be one of the main reasons why spatial behaviour of males is so diversified in this group of animals. Not surprisingly, territoriality has recently been found in some populations of species which were traditionally considered non-territorial (e.g., Miura 1984; Marchinton and Atkeson 1985; Apollonio 1989; Carranza et al. 1990).

The behaviour of Chinese water deer (*Hydropotes inermis*) introduced in Europe has been described by various authors (Cooke and Farrell 1981, 1983; Feer 1982; Stadler 1988, 1991). The male deer is territorial, at least in the population in England (Cooke and Farrell 1981, 1983; Stadler 1988, 1991). The most detailed study was conducted by Stadler (1991) at Whipsnade Wild Animal Park. He reported that adult male water deer hold small permanent territories that average 0.98 ha in size and show the highest degree of territoriality in the rutting season. A similar pattern of seasonal fluctuation in male territoriality is also well reported in another small deer, the roe deer *Capreolus capreolus* (Hennig 1962; Kurt 1968; Bramley 1970; Stüwe and Hendrichs 1984; Chapman et al. 1993). None of these authors, however, has specifically probed the effect of female movement on male territoriality. Here we report on the territorial system in a natural population of the water deer in China, where males appeared to space their mating territories and showed daily fluctuation in their territoriality according to the distribution of females.

Material and methods

The research area was located at 29°10′ N and 116°03′ E at Jiniushan Hill, Yongxiu County, Jiangxi, China (Fig. 1). The mean annual temperature is 17 °C (range: –4 to 40 °C). The annual precipitation is 1 400–1 500 mm, 48.2% of which falls in April, May and June. The habitat of the water deer is the grassland and hills at the mouth of Ganjiang River. Jiniushan Hill is a low, narrow zone slightly elevated above the grassland with an area of about 1 km^2. It is submerged annually for 2–4 weeks in the summer, when all the deer take shelter in the higher Jishan Hills.

This research was conducted from May 1988 to April 1989. Most of the observations were centered on 22 individually identified deer (11 males and 11 females) on Cluster 2 (Fig. 1) from October 1988 to January 1989, a period that included the mating season of the deer. The activity of the deer during the day time was composed of two active periods (dawn to 10.00 h and 15.30 h to dusk), when the deer were in move, and one resting period (between 10.00 h and 15.30 h), when most deer were ruminating, resting or sleeping. We hence divided our daily observations into three sessions: morning (7.00 h–10.00 h), afternoon (12.00 h–13.30 h), and evening (15.30 h–17.30 h). Individuals were identified by their facial marks with a 10×30 NIKON spotting scope. Males (denoted by "M") possessed tusks and thus were distinguished from females (denoted by "F"). We used the focal animal and scan sampling methods to collect observational data (Altmann 1974). We chose focal animals each day and alternated among these animals every 10 min. We also scanned animals four times a day (at 8.00 h, 11.00 h, 13.00 h and 16.30 h), two of which were in the active period and the other two in the resting period, and recorded their locations. To determine the relationship between male territoriality and female distribution, we defined and measured the following parameters:

1. Territory size (TSZ): defined as a defended area. We dotted the locations where a male marked or drove out invading males on a topographic map, and calculated the area using the minimum polygon method (Mohr 1947).

2. Territory stability (TST): defined as the percentage of time spent, for the holder, within his territory (see Owen-Smith 1975). This index is intended to show an animal's tenacity in territory-holding. It was measured separately for the active and resting periods using the percentage of scans that an animal was observed within its territory.

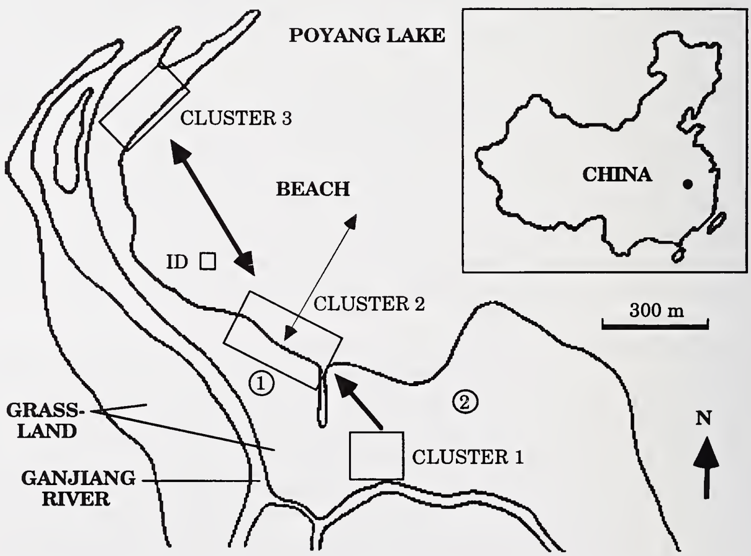

Fig. 1. The research area. Cluster 1, 2 and 3 were the approximate locations of the three territorial grounds. IT indicates the individual territory of M12. Thick arrowed lines represent the movement of males between territorial grounds. The thin arrowed line shows the movement of females, who regularly visited Cluster 2, between the resting place and feeding ground. Jiniushan Hill and Jishan Hills are marked with (①) and (②), respectively.

3. Female occurrence frequency (FOF): defined as the average number of females per scan on a territory and used for evaluating the quality of the territory.

4. Female density (FD): defined as female occurrence frequency per hectare of territory. It was obtained by using FOF divided by the territory size and multiplied by 10^4.

Also, we searched other areas regularly to monitor the direction and sequence of the movement of males and females between territorial grounds. The word "cluster" was used to indicate a territorial ground where several males spaced their territories closely (within 50 m between the nearest points of two neighbouring territories).

Results

Establishment of territories

Five females and three males were found at Cluster 1 (Fig. 1) on 25 October 1988. The females ranged over an area of 20–40 ha and intensively used a 5 ha core area for feeding and resting. Females' home ranges overlapped extensively and no areas were defended. Each of the three males, however, occupied an exclusive area of about 0.5 ha by driving out invaders and marking (see Sun et al. 1994).

On 3 and 4 November 1988, all five females moved to Cluster 2 (Fig. 1), coinciding with the onset of grass-cutting activity of local farmers at Cluster 1. The three males came to Cluster 2 two or three days later and began to set up new territories. By 12 November, nine males and six females from other areas, as a result of continued grass-cutting activity of local people, had also joined Cluster 2. Having failed to set up a territory, male M13 left Cluster 2 for Cluster 3, which had been divided into territories by six males and used as a feeding ground by seven to nine females. Male M11 deserted his territory on Cluster 2 after females previously visiting his territory had shifted to other places. Male M12 set up an individual territory of 0.5 ha on a quiet short grass area (Fig. 1) in early November. He stayed with F12, who was seldom out of the territory throughout the mating season.

Correlates of territories

During the mating season, all adult males were territorial. For the 11 territories on Cluster 2 (Fig. 2), the mean size was 4,980 $m^2 \pm 1,260$ (SD), with FOF 0.84 ± 0.48 (SD) and FD 1.64 ± 0.77 (SD). The mean TST was 96.85% in the active period and 74.14% in the resting period (Tab. 1). Positive associations between FOF and TSZ ($r = 0.699$, $P < 0.05$), FOF and FD ($r = 0.885$, $P < 0.01$), and FD and TST during the active period ($r = 0.768$, $P < 0.05$) were detected using the Pearson's product-moment correlation coefficient. The correlation between FOF and male TST at active period was marginally significant ($r = 0.558$, $P \approx 0.05$). Other correlations in the pairwise comparisons of these parameters failed to show any significance. Also, female density over the 11 territories was not differently from the uniform distribution (Kolmogorov-Smirnov goodness of fit test, $D = 0.64$, $N = 11$, $P = 0.07$). TST was significantly higher during the active period than the resting period (Wilcoxon paired-sample test, $T = 3$, $N = 11$, $P = 0.006$).

Use of territories

Females used the quiet beach of the lake as resting place and came to males' territorial grounds as feeding sites. The 11 regular female visitors on Cluster 2 came to feed at 15.30 h each day, resulting in a locally high density (from 0.13/ha on the beach to 1.64/ha on the cluster) of females on the territorial ground. They scattered across the 11 territories and could freely move between territories without interference from males. The ter-

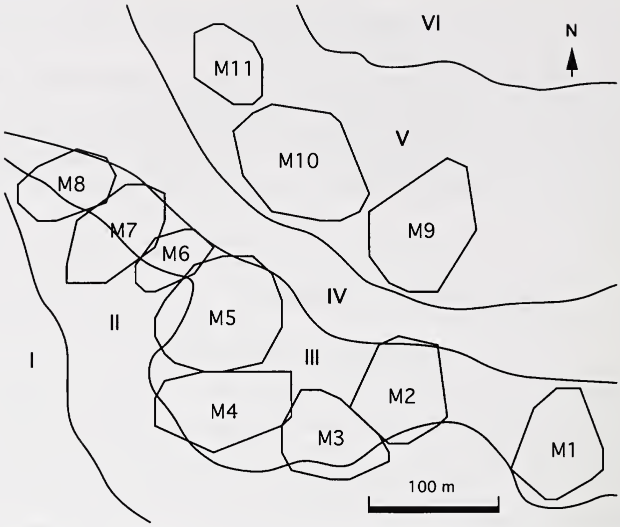

Fig. 2. The locations, shapes, and sizes of the 11 territories on the territorial ground, Cluster 2. Vegetation types are also shown: I. *Carex*-dominant zone; II. *Carex* and *Artemisia*-dominant zone; III. *Artemisia*, *Kalimeris* and *Viola*-dominant zone; IV. sparse *Artemisia* Zone; V. *Kalimeris* and *Artemisia*-dominant zone; VI. beach.

Table 1. Territory sizes, territorial stabilities, occurrence frequencies of females and female densities of the 11 territories on Cluster 2 during the mating season. (The numbers in parentheses are the number of total observations.)

Territory Holder	Territory (TSZ) (m)	Female Occurrence Frequency (FOF) (Females/scan)	Female Density (FD) (Females/ha)	Territorial Stability (TST) (%)	
				Active Phase	Resting Phase
M1	3700	0.78(9)	2.10	100.0(6)	100.0(5)
M2	4010	0.88(25)	2.19	100.0(17)	81.3(16)
M3	3940	0.82(11)	2.08	100.0(9)	57.1(7)
M4	6060	1.15(26)	1.90	100.0(17)	81.3(16)
M5	6840	1.76(29)	2.57	100.0(19)	88.9(18)
M6	2990	0.21(14)	0.72	100.0(10)	90.0(10)
M7	4990	0.29(31)	0.58	86.4(22)	100.0(19)
M8	4280	0.17(23)	0.41	88.9(9)	28.6(7)
M9	6300	1.50(8)	2.38	100.0(6)	83.3(6)
M10	6710	0.82(22)	1.22	90.0(20)	55.0(20)
M11	4960	0.94(18)	1.90	100.0(6)	50.0(6)

ritories were divided into two sub-clusters of territories by a non-territorial zone, where few plants grew well (Fig. 2). Females frequently travelled through that area, but did not linger there. Also, females feeding on Cluster 2 were rarely seen outside of the 11 territories. They went back to the beach at 10.00 h the second day and rested there until 15.30 h. Activities of the deer at night were not clear due to lack of night-vision equipment. The resting place was 800–1,500 m away from the feeding ground, and the ranging area of females was estimated to be 50–120 ha. Four females rested in tall grass near Cluster 2 after they transferred from Cluster 1. They shifted their resting places to the beach after the plants used as cover were cut.

Males were rarely observed out of their own territories during the active period. When females left their feeding ground for the beach, some males vacated their territories to join the females. Males often pursued and courted females on the beach, but no matings were observed. These males always returned alone to their territories by 15.30 h, before females came back to feed on the territorial ground. Males usually marked their territories upon their return. A few males remained in their territories throughout the resting period. They were seen to court females which passed by infrequently.

From the onset of the non-mating season at the end of January, the frequencies of marking behaviour in males and chases between males during the active period both tapered from 4.0/hr in the mating season down to less than 0.5/hr in April, indicating a significant drop in male territoriality.

Discussion

Female ungulates are usually more sensitive to disturbances than males (Clutton-Brock et al. 1982, 1989; Deutsch and Nefdt 1992). In our study, the change of the territorial ground from Cluster 1 to Cluster 2 was initiated by females. The energetically costly daily travel between the beach and the feeding ground could have been avoided (like the case of F12), had there been no disturbance. Thus, grass-cutting activity of local farmers seemed to be responsible for the shift of the females from tall grass areas at Clusters 1 and 2 to the quiet beach. The time lag of the males' movement to Cluster 2 indicated that the subsequent relocation of males' territories was initiated by the change in female home range.

The density of females in some cervids appears to play a pivotal role in males' assessment of whether and where to set up territories (Bramley 1970; Miura 1984; Carranza et al. 1990). This is supported by our study. First, all the 11 territories on Cluster 2 were located in areas with a high density of females, leaving the areas not frequented by females, like the non-territorial zone between the two sub-clusters (Fig. 2), unoccupied. Second, territories may be spaced in close proximity or solitarily, but no territories were located in areas without females, even if the food was abundant (Sun 1989). Males may desert a territorial ground if they failed to obtain a turf with a high female density (like the case of M13) or if females formerly feeding on their territories shifted to other places (like the case of M11). Finally, the positive correlation between female density and territorial stability in the active period provided a strong evidence that males' tenacity in holding territories was determined by female density. When fewer females appeared in territories during the resting period, males were more inclined to leave their territory to follow females.

The positive correlation between the size and occurrence frequency of females of a territory can be explained by the moderate evenness in female density over the 11 territories on Cluster 2. That is to say a large territory may include more females, which is similar to the case in roe deer (*Capreolus capreolus*) (Bramley 1970) and other vertebrate species (see review in Davies 1991 and Stamps 1994). It follows that males should defend a territory as large as possible. This tendency, however, is counteracted by the efficiency in territorial defense, which decreases as the size of a territory increases and eventually sets the upper limit of the size (Gosling 1981). Compared with other ungulates of similar body size (e. g., Estes 1967; Walther 1972; 1978; Hofmann 1973; Dunbar and Dunbar 1974; Dubost 1980; Kingdon 1982), the territory of the water deer in our study was very small, only half of that reported by Stadler (1991). This may be due to the difference in female ranging behaviour between the two populations: females used a larger area in our study than in Stadler's study. It is suggested that large ranging areas of females make it less possible or worthwhile for males to defend large territories that include the whole ranging areas of females (Barrette 1977; Gosling 1981). A more efficient way to gain access to reproductive opportunities may be to wait at some places where females occur most frequently (Bradbury 1981). Hence, male territory clusters can be expected in areas where female densities are high, the extreme form of which is lek (Bradbury 1981). This may account for the formation of territorial grounds in the water deer. The small territory size may be a result of intense competition among males in partitioning the limited feeding ground frequented by females. In these small and clustered territories, females are easily prompted to move between the territories, which did not favour males' interfering with females (Clutton-Brock et al. 1988; 1989; Clutton-Brock 1989; Stillman et al. 1993). This may be the reason why male water deer showed no attempts to prevent females from moving freely between territories both in Stadler's (1991) study and ours. The territorial system in the water deer looks somewhat like a lek (Buechner 1961; Leuthold 1966; Schuster 1976; Fryxell 1987; Clutton-Brock et al. 1988). However, the fact that males occupied relatively large territories (compared with lekking animals), which included the main food resource, was contrary to the criteria of a lek (Bradbury 1981, 1985; Clutton-Brock et al. 1988; Wiley 1991). This territorial system resembled the mating territory in some African ungulates (Estes 1974; Gosling 1986), which is considered an intermediate form between resource defense territories and classical leks (Clutton-Brock 1989).

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Zusammenfassung

Der Einfluß der Verteilung von Weibchen auf die Territorialität der Männchen beim chinesischen Wasserreh (Hydropotes inermis)

Das chinesische Wasserreh (*Hydropotes inermis*) wurde in seinem heimischen Lebensraum am Poyang See, Jiangxi, China, studiert. Diese Studie behandelt das Territoriumsverteidigungsverhalten während der Paarungszeit von Ende Oktober bis Januar. Während dieser Zeit war der tägliche Aktivitätszyklus von Weibchen folgendermaßen: Aktivitätsperiode von Tagesanbruch bis Mitte Vormittag, Ruheperiode bis Mitte Nachmittag und Aktivitätsperiode bis Einbruch der Dunkelheit. Die Weibchen verbreiteten sich weit voneinander im Sand entlang des Sees während der Ruheperiode. Während der Aktivitätsperiode liefen sie hinüber zum Weidegelände, das in der Nähe unter Territoriumsherrschaft der Männchen gehalten wurde. Die meisten Territorien der Männchen waren eng nebeneinander, und die Männchen versuchten die Weibchen zu umwerben, während sie auf ihren Territorien grasten. Wenn alle Weibchen das Weidegelände verließen und zurückkehrten zur Sandfläche entlang des Sees um zu ruhen, folgten einige Männchen den Weibchen nach, während andere in ihren Territorien auf dem Weidegelände verblieben.

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