Location of rut stands vs. mating opportunities in Przewalski’s gazelle: A field test of the “Resource-based Hypothesis” and “Female Traffic Version of the Hotspot Hypothesis”

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Abstract We studied the mating tactics of Przewalski’s gazelle on the Qinghai-Tibetan Plateau from 2002 to 2005. Przewalski’s gazelle is a cluster mating animal whereby female groups, including juveniles, travel to and from their resting grounds along fixed routes and dominant males stand on or near these travel routes during rut. To explain rut patterns in male gazelles, we tested predictions arising from the “Resource-based Hypothesis” and “Female Traffic Version of the Hotspot Hypothesis”. We marked the location of each rut stand and female travel route, measured food availability in each rut stand and recorded the mating opportunities of rut stand owners. We also conducted a field experiment to force female groups to change their daily travel route, and observed whether males abandon their original rut stands and shift their rut stands to new travel routes of females during the 3\textsuperscript{rd} rut. We found that: (1) male gazelle defending rut stands closer to a female travel route had a higher chance of mating; (2) food resources within rut stands had no effect on mating opportunities of the rut stand owner; (3) when the female travel route was obstructed, female groups changed grazing sites, and all males abandoned their original rut stands and defended new rut stands along the new female travel route. In conclusion, the location of rut stands in relation to female travel routes is the ultimate factor for consolidating mating opportunities in male gazelle, supporting the “Female Route Version of Hotspot Hypothesis” \cite{Current Zoology 57 (6): 701–708, 2011}.

Keywords Procapra przewalskii, Rut stand, Hotspot hypothesis, Mating opportunity, Food availability

The defense of rut stands is one mating tactic in ungulates whereby a male occupies and chases away male invaders from the defended stand \cite{Chapman and Chapman, 1975}. Many hypotheses have been suggested to explain the evolution of breeding systems in clustered mating animals and can be divided into two categories. The first category of hypotheses emphasizes the impact of environmental factors such as food resources or special land marks on breeding system evolution in animals. Pelletier et al. \textsuperscript{(1999)} and Brivio et al. \textsuperscript{(2010)} reported that food resources are important for both sexes during rut and that males and females in alpine ibex Capra ibex and bighorn sheep Ovis canadensis spend more time foraging when they are not engaged in mating. One of the most studied hypothesis for this category is the “Resource-based Hypothesis”, which suggests that breeding sites should be formed close to or at resources used by females, for example at feeding sites or nesting sites \cite{Alexander, 1975; Takács et al., 2002; Loyau et al., 2007}.

The second category of hypotheses emphasizes the impact of the biological characteristic of species itself on the evolution of breeding systems such as attraction of males to females or a cluster of females to which males are attracted. For example, the “Hotspot Hypothesis” emphasizes the male solution to the ‘mate encounter problem’ \cite{Lill, 1976} and suggests that males should form rut stands either in areas (1) where there is a high degree of overlap of female home range \cite{Bradbury et al., 1986}; (2) where females spend most of their time \cite{Apollonio et al., 1990}; or (3) where there is high female traffic \cite{Clutton-Brock et al. 1988, Westcott, 1997}. However, this hypothesis also suggests that food resources should not be considered and even in the absence of resource gradients hotspots could arise from overlapping female home ranges \cite{Höglund and Aalatalo, 1989}.
1995; Bradbury et al., 1986). Based on the traditional “Hotspot Hypothesis”, “Female Traffic Version of the Hotspot Hypothesis” was proposed in the study of neotropical frugivorous birds, which suggests that breeding territories (leks) of the birds could occur in areas of high female traffic (Westcott, 1997).

We studied the mating tactics of male Przewalski’s gazelle Procapra przewalskii on the Qinghai-Tibetan Plateau from 2002 to 2005. We first tested predictions of the “Resource-based Hypothesis” in the field: (1) males defend rut stands at foraging sites and (2) change of mating opportunity of male gazelle correlated with food availability in their rut stands. We also tested predictions from the “Female Traffic Version of the Hotspot Hypothesis” in the field: (1) male gazelle would defend rut stands on or near the travel route of females for higher encounter rate and consequently mating rate and (2) when females change their daily travel route males change the location of their rut stands accordingly.

1 Methods and Materials

1.1 Study areas and animals

Our two study areas (Hudong-Ketu and Yuanzhe) are located in the eastern part of the Qinghai Lake drainage (36°28’–38°25’N, 97°53’–101°13’E) on the Qinghai-Tibetan Plateau (Fig. 1). These areas are inhabited by two separate Przewalski’s gazelle populations, as indicated by recent micro satellite DNA work that showed no exchange occurs across the 20 km separation zone (Yang et al., 2011). The area ranges from 3000–3800 m above sea level. The activity ranges are 4.7 km² in Yuanzhe and 8.0 km² in and Hudong-Ketu (Li et al. 2011, in press). The climate is characterized by dry and cold winters, strong winds, high levels of solar radiation and a short growing season. The average annual temperature is 1.1°C (range: –31–25°C) and annual precipitation varies from 395 to 412 mm. Most precipitation falls between June and September. In Hudong-Ketu there is a mosaic of (1) steppe with dominant plants spear grass Achnatherum splendens, Leymus secalinus and Stipa purpurea; (2) desert shrub land with dominant plants such as Ephedra intermedia and Artemisia desertorum; and (3) alpine shrub land with dominant plants asa Sabina vulgaris and Salix ortreoha. Vegetation in Yuanzhe is alpine meadow with dominant spear grass and stipa including Stipa krylovii, S. breviflora and S. breviflora.

Przewalski’s gazelle is a rare and critically endangered species and had been classified as “Critically Endangered” by the IUCN (Jiang et al., 2000; Jiang et al., 2001; Jiang and Wang, 2001; Hilton-Taylor, 2000). There were once fewer than 300 individuals found in around Qinghai Lake in the early 1990s (Jiang et al., 2000). Przewalski’s gazelle live sexually segregated out of rut season and group size changes across the seasons; however, the two sexes form mixed groups approximately one month before the rut (Lei et al., 2001a, 2001b).

![Fig. 1  Study areas Hudong-Ketu and Yuanzhe to the east of Qinghai Lake](https://academic.oup.com/cz/article-abstract/57/6/701/1791835)

During rut from early December to late January sexually mature females, including juveniles, travel from their resting ground in the early morning to foraging grounds, returning to their resting ground in the late afternoon following a fixed route and as one large group (You and Jiang, 2005). As rut begins sexually mature males fight for rut stand positions and winners establish rut stands first. Males mark their rut stand by digging small pits around the boundary and spraying urine or fecal pellets into these. Males call ‘En-hen’ or “A’gang” while patrolling the stands and call “Al-gan, Al-gan” while chasing away intruders. Rut stand owners defend their rut stands during the daytime throughout the whole rut. Males that did not acquire a rut stand become floaters that remain away from the rut grounds during the rut (You and Jiang, 2005).

We chose the populations around Hudong-Ketu (in the rut season of 2003) and Yuanzhe (in the rut seasons 2003–2004) as our study populations because these two populations comprise more than half of all known individuals remaining in the wild (Table 1).
Table 1  Study groups and field work schedule

| Rut     | Number of dominant males | Female group size (n) | Rut onset date | Rut diminishing date | Observation time (Day/Min) |
|---------|--------------------------|-----------------------|----------------|----------------------|---------------------------|
| 1st rut | 6                        | 36                    | Dec. 21, 2002  | Jan. 12, 2003        | 32/1784                   |
| 2nd rut | 3                        | 27                    | Dec. 24, 2003  | Jan. 9, 2004         | 27/1824                   |
| 3rd rut | 3                        | 28                    | Dec. 14, 2004  | Jan. 9, 2005         | 31/2087                   |

1.2  Rut stand location and female travel route

Fecal pellet and urine marker traces around each rut stand were recorded with a GPS receiver to define the boundary of a rut stand at the end of each rut season. We then plotted geographic coordinates of fecal pellet and urine marker on a digital map of the study area using ArcView 3.2. We created polygon themes to determine the position and shape of each rut stand based on those geographic coordinates in both study areas. All rut stands were named in order of their establishment by rut stand owners (Figs. 2–4). We tracked females from a distance of 100–200 m and recorded their travel route on rut stand areas with a GPS receiver at the beginning of each rut and then plotted geographic coordinates of female travel route lines on a digital map of the study area using ArcView 3.2. If a female travel route transected through a rut stand we defined the distance between the rut stand and female travel route as zero; if the female travel route did not transect through a rut stand we used the measure tool in ArcView to measure the distance between the line theme of the female travel route and geometrical center of the polygon theme of the rut stand.

1.3  Mating opportunity

All individuals could be seen at any time because of the openness of the steppe landscape. We observed behaviors of dominant gazelle within rut stands through a hide with binoculars (8×42). Behavior (mount, copulation and others) of all rut stand owners and female groups were instantaneously recorded using scan sampling methods at 10-min intervals with SJ-1 Event Recorder (Martin and Bateson, 1993; Jiang, 1999). Because males never left their rut stands during the day, behavioral sampling lasted from 07:00–19:00 h each day during the entire rut. If we observed that one rut stand was defended by a male gazelle and lasted for one day, we defined it as the beginning of a rut, if no mounting was observed during three continuous days, we assumed that the rut season had ended and we stopped behavioral sampling for that rut season.

Mating opportunities were defined as a male gazelle mounting or copulating with a female. Mount was defined as a male gazelle standing and moving on his hind legs following a female gazelle, tried to put his forelegs on the back of the female. Copulation was considered successful when a male gazelle stood on by his hind legs and put his forelegs on the back of a female, followed by copulation and a thrust. Sometimes male gazelle puts their forelegs on the back of female gazelle but did not copulate.

Total behavioral observations across six rut stands were conducted for 1784 min over 32 continuous days between December 2002 and January 2003 at Hudong-Ketu (which we defined as the 1st rut). In the winter of 2004, local herdsmen released hundreds of domestic sheep into the rut grounds of the gazelle in Hudong-Ketu and gazelle were forced to change their rut ground to an unknown place. Consequently, we had to shift our study to the Yuanzhe area, where total behavioral observation across three rut stands was conducted for 1824 min over 27 continuous days between December 2003 and January 2004 (defined as the 2nd rut) and 2087 min over 31 days between December 2004 and January 2005 (3rd rut) (Table 1).

Fig. 2  Rut ground in Hudong-Ketu during the 1st rut season

Arrowed lines are female travel routes on rut grounds; real lines are grassland fence lines. Shaded areas represent rut stands of male Przewalski’s gazelle and No. 1 to No. 6 were the order of rut stand establishment.
1.4 Food availability

To study whether food resources influence the choice of location of rut stands we measured the aboveground biomass using systematic sampling methods at the beginning of each rut. Sampling points were set every 10 m in a chessboard fashion across the two study areas. Each sampling point was numbered. At each sampling point we placed a sampling quadrate of \(100 \times 100\) cm\(^2\) on the ground, composed of 100 small grids, and we measured herbage coverage as percent grid covered by plants in the quadrate and height of plants at the four corners of the quadrates. The log (coverage \(\times\) height) was treated as the food availability index in the corresponding rut stand (Carranza, 1995). In total, 213 and 136 samples were measured in Hudong-Ketu and Yuanzhe areas respectively.

1.5 Female travel route obstructing experiment

To see whether males alter the position of the rut stand once female travel routes change, we carried out a female travel route obstructing experiment at the beginning of the 3rd rut. There were two entrances where female groups entered the rut stand area and we enclosed both entrances with red plastic rope (Fig. 4). We then recorded whether the rut stand owners abandoned their original rut stands and shifted their rut stands to the new female route.

1.6 Data analysis

We used SPSS 15 (SPSS Inc., Chicago, USA). The data biased significantly from the normal distribution (one sample Kolmogorov-Smirnov test, \(P<0.05\)) so we tested differences using the Kruskal-Wallis H-test. We tested for differences in food resources within each rut stand and mating opportunities (including successful matings) of dominant male gazelle in both study areas with a Kruskal–Wallis H-test. We tested the correlation between mating opportunities (including successful matings) and food resources in the corresponding rut stand using two-tailed Spearman’s correlation tests. We also performed a correlation between mating opportunity (including successful matings) and location of rut stand in relation to female travel route. \(P<0.05\) was considered significant for all statistical tests.

2 Results

There were 36 females gathered in one group in Hudong-Ketu during the 1st rut. Twenty-seven females gathered in a group in Yuanzhe during the 2nd rut and 28 during the 3rd rut (Table 1). Males established six rut stands during the 1st rut at Hudong-Ketu and three rut stands during the 2nd and 3rd ruts at Yuanzhe.

2.1 Location of rut stand and female travel route

Female groups formed approximately two weeks before the rut. Females traveled between the daily fora-
ging habitat and night resting habitat 1–2 km away along fixed routes over the three years. Przewalski’s gazelles in Hudong-Ketu area rested within sand dunes during the night and came to grassland for grazing during the day during the whole rut season. Female gazelle at Yuanzhe spent their day time in the foraging area where they were courted and mated by males when they grazed through rut stands of males.

As rut started males established rut stands along the travel route of the females through fighting. Six rut stands were defended by dominant gazelles at Hudong-Ketu, five of which were on the female travel routes during the 1st rut (Fig. 2). There were three rut stands defended by dominant males at Yuanzhe during the 2nd and 3rd ruts. All rust stands were positioned along the female travel route except the third rut stand during 2nd rut (Figs. 3–4).

### 2.2 Mating opportunity and location of rut stand in relation to female travel route

Gazelle that defended rut stands on the female travel routes had more mating opportunities than those defending rut stands off the route. The mating opportunities of territorial males differed significantly among rut stands (Kruskal-Wallis H-test; Hudong-Ketu: $\chi^2=212.00$, $df=5$, $P<0.01$; Yuanzhe: $\chi^2=135.00$, $df=5$, $P<0.01$). The opportunity to mate for dominant males was inversely correlated to the distance between the geometric center of the rut stand and the female travel route (Two-tailed Spearman’s correlation test; Hudong-Ketu: $r=-0.91$, $n=31$, $P<0.01$; Yuanzhe: $r=-0.71$, $n=65$, $P<0.05$) (Table 2). Correlation analysis showed that mating opportunities were correlated with the distance between the rut stand and female travel routes (two-tailed Spearman’s correlation test: $r=-0.8$, $n=12$, $P<0.05$, Table 3).

| Table 2 | Mating opportunities of dominant males, food resource index within rut stands and the location of rut stands in relation to female travel routes |
|---------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Rut season | Dominant male | Mating opportunity (counts) | Mountings (counts) | Copulations (counts) | Successful mating | Food Resource Index (Mean ± SE) | Distance (m)* |
|-----------|----------------|----------------------------|------------------|---------------------|-------------------|-----------------------------|-------------|
| 1st rut | 1 | 253 | 217 | 36 | 3.24 | 2.01 ± 0.43 | 0 |
| | 2 | 51 | 46 | 5 | 2.21 | 2.03 ± 0.46 | 165 |
| | 3 | 246 | 218 | 28 | 2.43 | 2.21 ± 0.58 | 0 |
| | 4 | 81 | 73 | 8 | 2.22 | 3.09 ± 0.13 | 0 |
| | 5 | 0 | 0 | 0 | – | 2.98 ± 0.24 | 200 |
| | 6 | 51 | 45 | 6 | 2.49 | 2.91 ± 0.15 | 375 |
| 2nd rut | 1 | 649 | 611 | 38 | 1.24 | 2.72 ± 0.20 | 0 |
| | 2 | 508 | 461 | 47 | 2.13 | 2.63 ± 0.18 | 0 |
| | 3 | 0 | 0 | 0 | – | 2.68 ± 0.21 | 370 |
| | 1 | 119 | 104 | 15 | 3.01 | 2.73 ± 0.72 | 0 |
| 3rd rut | 2 | 58 | 58 | 0 | 0.00 | 2.68 ± 0.93 | 0 |
| | 3 | 74 | 74 | 0 | 0.00 | 2.81 ± 0.29 | 0 |

*The distance between rut stand and female travel route. * Successful mating = copulating/mating opportunity x 100

| Table 3 | Successful mating, mating opportunity and distance between rut stands and the female travel route |
|---------|----------------------------------------------------------------------------------------------|
| Successful mating | Correlation Coefficient | 1.000 | 0.079 | 0.200 |
| | Sig. (2-tailed) | 0.000 | 0.828 | 0.580 |
| | n | 10 | 10 | 10 |
| Mating opportunity | Correlation Coefficient | 0.079 | 1.000 | -0.802** |
| | P (2-tailed) | 0.828 | 0.000 | 0.002 |
| | n | 10 | 12 | 12 |
| Distance | Correlation Coefficient | 0.200 | -0.802** | 1.000 |
| | P (2-tailed) | 0.580 | 0.002 | 0.000 |
| | n | 10 | 12 | 12 |

** Pearson Correlation is significant at the 0.01 level (2-tailed).
2.3 Food availability within rut stand and mating opportunity of dominant male

Correlation analysis showed that mating opportunities in each rut stand were not related to the food resource index of the corresponding rut stand (Two-tailed Spearman’s correlation test: \( r = -0.17, n = 12, P = 0.38, \) Table 4), though there was a difference in the food availability index among rut stands (Kruskal–Wallis H-test: \( \chi^2 = 147.00, df = 11, P < 0.05 \)).

2.4 Female travel route obstructing experiment

After obstruction the female group changed their route in the paddocks (Fig. 4). Consequently, males abandoned their original rut stands immediately and established new rut stands on the new female travel route.

3 Discussion

Rut stand grounds were defended by males in the foraging sites of females; however, food resources within rut stands had no clear impact on the mating opportunities of rut stand owning males. Except for third rut stand, other rut stands were located on or close to female travel routes. All dominant males abandoned their rut stand to defend new rut stands according to altered female travel routes in the female travel route obstruct experiment. These findings indicate that the moving path of females during rut is a hot spot that attracts male gazelle.

Some studies suggest that food resources are important for both sexes during rut (Pelletier et al., 1999; Brivio et al., 2010), and essential for dominant males to obtain mating opportunities (Loyau et al., 2007). Our results also show that food resources are important for females because the female group spent of the majority of each day grazing; dominant males ate little during the whole rut season. Statistical analysis suggested that food resources had no clear impact on mating opportunity in dominant male gazelle. Such a result may be because female groups grazed and moved through most of the rut stands following a fixed route (Figs. 2–4). During peak foraging times there were no clear differences in the chances that a dominant male would encounter a female because grazing females normally do not accept courting males. Females would rest after a feeding bout and which rut stand the female group stopped to rest in had a clear impact on the chance of encountering a female. The success of a dominant male was determined by the location of his rut stand: the closer the rut stand was to the moving path of females, the more likely it was that the female group would stop grazing and rest. Though rut stands were set up in foraging sites, the Food Resource-based Hypothesis cannot explain the observed mating tactics of Przewalski’s gazelle.

Territory characteristics such as territory size, tenure or location affect the breeding success of dominant males (Cutts et al., 1999; Bart and Earnst, 1999). We did not study the breeding success of male Przewalski’s gazelles here, but we did find that the location of the rut stand correlated with mating opportunity. For males, solving the ‘mate encounter problem’ is fundamental to securing mating opportunities (Lill, 1976). As the “Hotspot Hypothesis” predicted, dominant gazelles established rut stands on or near sites with high female traffic. To understand why males distributed their rut stands based on female travel routes, rather than some other aspect of female distribution, two points are important. First, female mate choice appears to be based on long-term sampling of males (Westcott, 1992; 1995). All sexually mature male gazelle fight each other to establish their social rank about two weeks before the first rut stand has been defended. Male fighting sites were on or near to the foraging sites of the female group; females had time to assess the males before rut. On the other hand, the fixed moving pattern of females made it possible for males to predict where to encounter

| Table 4 Successful mating, mating opportunity and available food resource index in rut stands |
|---------------------------------------------|-----------------|-----------------|-----------------|
| Successful mating                          | Correlation Coefficient | 1 | 0.054 | -0.347 |
|                                           | Sig. (2-tailed)       | 0.000 | 0.881 | 0.326 |
|                                           | \( n \)              | 10 | 10 | 10 |
| Mating opportunity                         | Pearson Correlation  | 0.054 | 1 | -0.171 |
|                                           | Sig. (2-tailed)       | 0.881 | 0.000 | 0.595 |
|                                           | \( n \)              | 10 | 12 | 12 |
| Food resource index                        | Correlation Coefficient | -0.347 | -0.171 | 1 |
|                                           | Sig. (2-tailed)       | 0.326 | 0.595 | 0.000 |
|                                           | \( n \)              | 10 | 12 | 12 |
receptive females. Studies have found that rut stand establishment order indicates the quality of male individuals (e.g. Kokko, 1997). These aspects mean that receptive females have sufficient time for mate sampling. Second, the location of sexually receptive females could be predicted by males. Because habitat available to Przewalski’s gazelles in winter was limited due to livestock, grazing was limited to unused livestock paddocks. The female travel route obstructing experiment suggested that the distribution of rut stands is a function of female travel routes. Male Przewalski’s gazelles had more opportunity to display along female travel routes.

We should point out here that livestock herding and grassland fences do interfere with the mating tactics of Przewalski’s gazelle. Rut grounds at Hudong-Ketu were flooded with domestic sheep in winter of 2003 which drove gazelle away from their traditional rut ground. We consequently had to observe another herd of gazelle at Yuanzhe. Additionally, the shape of rut stands defended by male gazelle should be of round or ellipse if the rut ground is free of obstruction for the male gazelle to establish rut stands; however, the shape of rut stands was either compressed by grassland fence lines during the 1st rut or male simply defended an entire fenced pasture paddock (thus the rut stands in the 2nd and 3rd rut appeared to be square shaped) (Figs. 2–4).

In conclusion, the rut in Przewalski’s gazelle is quite unique and the night resting grounds and foraging rutting grounds are separated by distance. Males return to the rut stands they first occupied. Females travelled to the same feeding ground during the whole rut season. Chemical signals in the urine and feces of males in rut may attract females to these “hot spots”. Aggregation of males on the travel route of females increases the chance of males encountering receptive females. These patterns can be explained by the “Female Traffic Version of the Hotspot Hypothesis”.

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