

Rut-induced changes in the activity budgets of male tropical ungulates: Eld's deer on Hainan Island

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Abstract Aspects of time budgets, activity patterns and rut-related changes in behavior are well documented in temperate ungulates; however, the application of this understanding to tropical and sub-tropical ungulate species has attracted less attention and remains an area that may re-shape our knowledge of ungulate behavior. Eld's deer *Cervus eldi hainanus* has a tropical and sub-tropical distribution on Hainan Island, China, and males have an extended rut exceeding five months during which they do not maintain harems or defend resources. We studied males from the only remaining population on Hainan Island, and describe rut-related changes in behavior by collecting data on time budgets and activity patterns. We show that male Eld's deer do not follow a strict crepuscular activity pattern, do not spend the majority of their time foraging and do not increase foraging nor display rut-induced hypophagia during rut, in obvious contrast to temperate ungulates. These results are discussed in light of current hypotheses explaining the proximate mechanisms governing feeding time in ungulates, while appreciating the need for further research [*Current Zoology* 58 (4): 536–540, 2012].

Keywords Activity, *Cervus eldi hainanus*, Eld's deer, Rut, Time budget, Tropical ungulate

Patterns of reproductive activity and behavior in ungulates are well developed research fields with a strong theoretical and empirical foundation. Aspects of time budgets, activity patterns, and rut-related changes in behavior are well documented in ungulates with the majority of our understanding of these dynamics arising from studies of temperate species inhabiting areas with harsh winters and large seasonal changes in weather. However, the application of this understanding to tropical and sub-tropical ungulate species has attracted less attention and remains an area of interest that may re-shape our knowledge of ungulate behavior.

Eld's deer *Cervus eldi hainanus* inhabit tropical and sub-tropical Hainan Island, China, and this species is critically endangered. Males attain maturity between one and two years of age, and the age at first copulation of females is approximately 500 days old (range 458–534 days) (Yuan et al., 1988; Song and Zeng 2003). Rutting behaviors first appear in mid-January and con-

tinue until the end of June (Yuan et al., 1988). Unlike the reproductive behavior of temperate deer, such as red deer (*Cervus elaphus*, Clutton-Brock et al. 1982) and sika deer (*C. nippon*, Miura 1984), male Eld's deer do not defend females or resources, though the dominant male usually maintains dominance for an extended period and sometimes the entire reproductive season. Males compete combatively to obtain access to females during the rut and instead of holding a harem, victors attempt to monopolize mating opportunities by guarding receptive females for two hours after copulation (Zeng et al., 2001).

Given this extended rut and different mating strategy from temperate ungulates, the purpose of our investigation was to describe rut-induced changes in behavior in male Eld's deer. Through analysis on diurnal activity patterns, behavior and levels of activity we then compare rut-induced changes in key behaviors, for example foraging, to that of temperate species.

1 Materials and Methods

1.1 Animals and study area

We collected data in 2005 and 2006 by observing Eld's deer at Hainan Datian National Nature Reserve, Hainan Island, China (19°49' N, 110°35' E; elevation 25 m a.s.l.). We conducted our study within a fenced 65 ha section of the reserve; the population within this area (see Table 1) is separated by a fence of two-meter-high wire netting from animals in other sections of the reserve. All our study animals were identifiable by unique ear marks made as yearlings. Vegetation within the reserve is comprised of 21% tree and shrub cover year

round (species include *Casuarina equisetifolia*, *Calophyllum inophyllum*, *Pandanus austrosinensis*, *Baeckea frutescens*, *Pinus merkusii*, and *Leptocarpus disjunctus*). However, ground cover and grass composition varies temporally (rutting months: grass and/or weeds (*Eupatorium catarium* 47.6%, *Panicum repens* 15.8%, and 20 species of weed 15.6%; non-rutting months: *Eupatorium catarium* 8.1%, *Panicum repens* 22.9%, and seldom eaten weed species 48.0%). There are natural small pools. The conditions satisfy the foraging and resting needs of Eld's deer. Pilose antlers are harvested in the first week of October each year.

Table 1 Age structure of Eld's deer present during the study

Year	Number of individuals			Males by age class (n)					
	Females	Males	Fawns	1.5 years	2.5 years	3.5 years	4.5 years	5.5 years	6.5 years and older
2005	20	12	11	5	1	1	4	1	0
2006	17	11	6	2	2	1	1	4	1

1.2 Data collection

Data were collected between 07: 00–19: 00 h during the rut (1 March to 20 May) and non-rut season (1 October to 30 November). Focal deer (range 3.5–6.5 years old) were observed with binoculars from a distance of 50–100 m to avoid possible effects of the observers on the behavior of males. Focal males were randomly selected at the commencement of each study year and then regularly observed during data collection seasons; however, due to animal illness, translocations and other management actions sufficient data spanning each season were available for only six different males each in 2005 and only two in 2006.

We observed one focal male at a time and using continuous sampling (Altmann 1974) recorded 1,812 deer-hours of data during the rut and 1,936 hours during non-rut for eight males in 2005 and 2006. Behaviors measured included lying (ruminating or resting), foraging (biting, chewing, browsing, grazing), standing (standing still, standing alert, standing ruminating), moving (walking, running), and other (fighting, marking, sniffing, wallowing, chasing, bellowing, copulating). We recorded a deer as lying if they were under the cover of shrubs and unable to be observed, a reasonable assumption since, if active, they would be easily visible amongst the shrubs. During rut, we assigned standing, moving and 'other' behaviors as rutting behavior as these activities are important for males to gain access to females in estrus (Willisch and Ingold 2007).

1.3 Data analyses

To compare rut and non-rut activity patterns, observations were averaged for each hour across the season. A chi-square independence test was used to compare seasonal differences across this data. We calculated the total time spent foraging, standing, moving, or 'other', and then divided this by the total time spent observing the deer to arrive at a proportional estimate for each behaviour for each male. Proportion data were transformed by taking the arc-sine square root (Zar, 1999) and analyzed using a mixed model ANOVA to show differences between rutting and non-rutting activity budgets. Given that only one male was observed in 2005 and then again in 2006 male ID was included as a random factor in the models instead of using repeated measure analysis. Year was also included as a random factor because of its likely effect on time budgets. Frequency data were calculated using only activity bouts greater than one min in length and analyzed using a Mann-Whitney U-test.

2 Results

Male Eld's deer were more active during the rutting period than the non-rutting period ($\chi^2 = 587.7$, $df = 11$, $P < 0.001$). Deer were active from 07: 00 h to after 18: 00 h and activity patterns followed a bimodal distribution with peaks in activity at 09: 00 h and 16: 00 h (Fig. 1). During the non-rutting season activity began around 08: 00–09: 00 h, and continued until 1800 h; peaks were

observed around 09: 00–10: 00 h and 15: 00–17: 00 h, with little to no activity between the hours of 12: 00–13: 00 h.

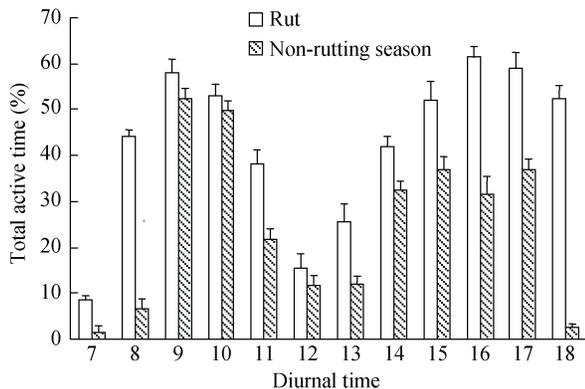


Fig. 1 Proportion (mean \pm SE) of time spent active by male Eld's deer

The proportion of time male deer spent engaged in lying, standing, moving, foraging and other behaviors changed seasonally. During the rut male Eld's deer spent a lower proportion of their time resting ($F_{1,318} = 291.7, P \leq 0.001$, Fig. 2) and more time standing ($F_{1,318} = 718.7, P \leq 0.001$), moving ($F_{1,318} = 573.4, P \leq 0.001$) and engaged in 'other' active behaviors ($F_{1,318} = 795.6, P \leq 0.001$). Collectively, males spent 26% of their time engaged in these active behaviors during the rutting period (Fig. 2). Conversely, no difference in the time spent foraging was observed across the rutting and non-rutting period as male deer consistently spent between 16.4% and 18.3% of their time engaged in this behavior ($F_{1,318} = 2.57, P = 0.11$).

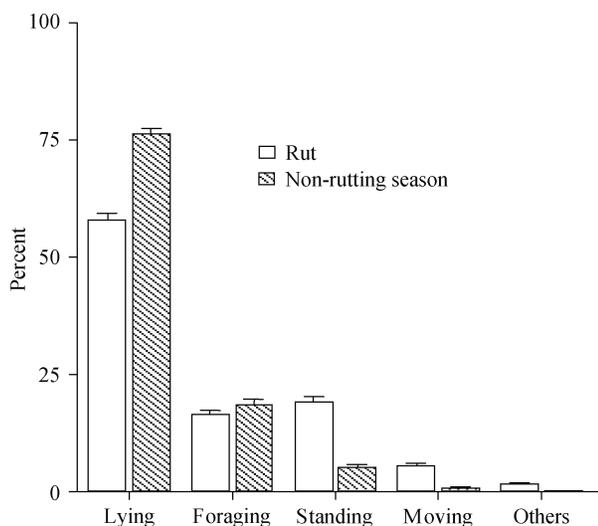


Fig. 2 The proportion (mean \pm SE) of time spent in different behaviors by male Eld's deer

We observed a significant seasonal pattern in the average length of active ($Z = -13.3, n = 1984, P \leq 0.001$) and inactive bouts ($Z = -17.6, n = 1676, P \leq 0.001$). The duration of active and inactive bouts was smaller during the rut than non-rut (mean active bout length: rut = 32 ± 1 min, non-rut = 53 ± 2 min; inactive bout length: rut = 36 ± 1 min, non-rut = 115 ± 5 min). A higher frequency of bouts during the rut compared to the non-rut was also observed (mean active bout frequency per 12 h diurnal period \pm SE: rut = 9.4 ± 0.4 ; non-rut = 3.3 ± 0.1 ; $Z = -14.1, n = 327, P \leq 0.001$; mean inactive bout frequency: rut = 10.2 ± 0.4 ; non-rut = 4.2 ± 0.1 ; $Z = -14.0, n = 327, P \leq 0.001$).

3 Discussion

Overall patterns of activity for male Eld's deer across the two study years showed they did not follow a typical crepuscular pattern with peaks in activity at 06: 00 and 18: 00 like other cervid species (Barrette, 1977; Collins et al., 1978; Eberhardt et al., 1984; Ivey and Causey, 1984; Beier and McCullough, 1990; Green and Bear, 1990). While the daily pattern of activity was bimodal (Fig. 1), males did not display the typical sunrise and sunset peaks in activity (Beier and McCullough, 1990) and instead were most active around 09: 00 h and 16: 00 h each day. A strict crepuscular pattern of activity has been linked to the presence of predators in the environment (Leuthold, 1977) and the fact that the reserve is protected from human harassment and potential predator may explain this deviation from expected behavior (Kamler et al., 2007; Loe et al., 2007). A study of translocated populations of Eld's deer inhabiting areas without predator control is needed to ascertain whether this is a true pattern for this species.

A rut-related change in the relative proportion of time spent engaged in different behaviors was found for all behaviors except foraging (Fig. 2). During rut, males spent less time lying and more time standing, moving and other active behaviors than compared to non-rut periods, which suggests that males were more active during rut than non-rut periods, as has been reported for a number of ungulate species (Kitchen, 1974; Georgii and Schroder, 1983). The obvious increase in standing and moving during rut indicates the importance of gaining access to females, and chasing and avoiding opponents (Relyea and Demarais, 1994). The most common behavior observed during the rut and non-rut was lying. This is consistent with sub-tropical ungulates (Dhungal and O'Gara, 1991), but in contrast to those

living in temperate zones where the dominant behavior is foraging (Green and Bear, 1990; Moncorps et al., 1997; Shi et al., 2003). The similar proportion of foraging time during rut and non-rut suggests that male Eld's deer do not exhibit obvious rut-induced hypophagia as occurs in many temperate ungulates (Miquelle, 1990; Komers et al., 1994; McElligott et al., 2003; Pelletier et al., 2009). This cannot be explained by any existing hypotheses offered to explain hypophagia in male ruminants, especially in those inhabiting temperate and arctic climates (Brivio et al., 2010), which further defines the special character of Eld's deer as a species of tropical and sub-tropical climates. The highly asynchronous distribution of females in estrus (the average interval where no female was in estrus was four days, unpublished data) and the roving strategy means males can spend as much time foraging as they look for females.

Concurrent with a general rut-related increase in activity, we found that the duration of 'active' bouts decreased and the frequency of these bouts increased. During rut, males are more likely to be engaged in rutting behaviors such as fighting and chasing other males. Rutting behaviors are disruptive to other behaviors such as foraging, lying and standing meaning that the duration of these behavioral bouts is likely to be smaller than without these interruptions, say, during the non-rutting season (Ruckstuhl, 1998). In addition, the dominant food source for Eld's deer during the rut was *Eupatorium catarium*, yet was *Panicum repens* during the non-rut. According to our measurement, the latter has a 42.5% higher crude fiber content than the former (67.6% vs. 25.1%), requiring a longer rumination time and longer periods of inactivity (Jingfors, 1982; Cederlund, 1989) and activity (Jingfors, 1982).

Acknowledgements Funding for this study was provided by National Nature Science Foundation of China (30430120). We followed guidelines for the use of animals in research as published by the journal *Animal Behaviour*. We thank staff at Hainan Datian National Nature Reserve for assistance during our field research with special thanks to Li Shanyuan and Xing Yichang who graciously contributed their time and effort during this study.

References

- Altmann J, 1974. Observational study of behavior: Sampling methods. *Behaviour* 49: 227–268.
- Barrette C, 1977. Some aspects of the behaviour of muntjacs in Wilpattu National Park. *Mammalia* 41: 1–34.
- Beier P, McCullough DR, 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildl. Monogr.* 109: 3–51.
- Brivio F, Grignolio S, Apollonio M, 2010. To feed or not to feed? Testing different hypotheses on rut - induced hypophagia in a mountain ungulate. *Ethology* 116: 406–415.
- Cederlund G, 1989. Activity patterns in moose and roe deer in a north boreal forest. *Holarctic Ecol.* 12: 39–45.
- Clutton-Brock TH, Guinness FE, Albon SD, 1982. *Red Deer: Behaviour and Ecology of Two Sexes*. Chicago: University of Chicago Press.
- Collins WB, Urness PJ, Austin DD, 1978. Elk diets and activities on different lodgepole pine habitat segments. *J. Wildl. Manage.* 42: 799–810.
- Dhungel SK, O'Gara BW, 1991. Ecology of the hog deer in Royal Chitwan National Park, Nepal. *Wildl. Monogr.* 119: 3–40.
- Eberhardt LE, Hason EE, Cadwell LL, 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. *J. Mammal.* 65: 404–409.
- Georgii B, Schroder W, 1983. Home range and activity patterns of male red deer (*Cervus elaphus* L.) in the Alps. *Oecologia* 49: 238–248.
- Green RA, Bear GD, 1990. Seasonal cycles and daily activity patterns of rocky mountain elk. *J. Wildl. Manage.* 54: 272–279.
- Ivey TL, Causey MK, 1984. Movements and activity patterns of female white-tailed deer during rut. *Proc. Ann. Conf. Southeast Assoc. Fish & Wildl. Agencies* 35: 149–166.
- Jingfors KT, 1982. Seasonal activity budgets and movements of a reintroduced Alaskan muskox herd. *J. Wildl. Manage.* 46: 344–350.
- Kamler JF, Jedrzejewska B, Jedrzejewski W, 2007. Activity patterns of red deer in Bialowieza National Park, Poland. *J. Mammal.* 88: 508–514.
- Kitchen DW, 1974. Social behavior and ecology of the pronghorn. *Wildl. Monogr.* 38: 1–96.
- Komers PE, Messier F, Gates CC, 1994. Plasticity of reproductive behaviour in wood bison bulls: When subadults are given a chance. *Ethol. Ecol. Evol.* 6: 313–330.
- Leuthold W, 1977. African ungulates: A comparative review of their ethology and behavioral ecology. *Zoophysiology Ecol.* 8: 1–307.
- Loe LE, Bonenfant C, Mysterud A, Severinsen T, Øritsland NA, 2007. Activity pattern of arctic reindeer in a predator-free environment: no need to keep a daily rhythm. *Oecologia* 152: 617–624.
- McElligott A, Naulty F, Clarke WV, Hayden TJ, 2003. The somatic cost of reproduction: What determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.* 5: 1239–1250.
- Miquelle DG, 1990. Why don't bull moose eat during the rut? *Behav. Ecol. Sociobiol.* 27: 145–151.
- Miura S, 1984. Social behavior and territoriality in male sika deer (*Cervus nippon* Temminck 1838). *Z. Tierpsychol.* 64: 33–73.
- Moncorps S, Bousset P, Reales D, Chapuis J, 1997. Diurnal time budget of the mouflon *Ovis musimon* on the Kerguelen archi-

- pelago: Influence of food resources, age, and sex. *Can. J. Zool.* 75: 1828–1834.
- Pelletier F, Mainguy J, Cote SD, 2009. Rut-induced hypophagia in male bighorn sheep and mountain goats: Foraging under time budget constraints. *Ethology* 115: 141–151.
- Relyea RA, Demarais S, 1994. Activity of desert mule deer during the breeding season. *J. Mammal.* 75: 940–949.
- Ruckstuhl KE, 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Anim. Behav.* 56: 99–106.
- Shi JB, Dunbar RIM, Buckland D, Miller D, 2003. Daytime activity budgets of feral goats *Capra hircus* on the isle of Rum: Influence of season, age, and sex. *Can. J. Zool.* 81: 803–815.
- Song YL, Zeng ZG, 2003. Reproductive characteristics of female Eld's deer in their natural range in Hainan Island, China. *Mammalia* 67: 47–53.
- Willisch CS, Ingold P, 2007. Feeding or resting? The strategy of rutting male Alpine chamois. *Ethology* 113: 97–104.
- Yuan XC, Lu BW, Li SY, 1988. Reproductive behavior of brow-antlered deer *Cervus eldi hainanus*. *Acta Theriologica Sinica* 8: 89–94.
- Zar JH, 1999. *Biostatistical Analysis*, 4rd edn. Prentice Hall, London.
- Zeng ZG, Song YL, Li SY, Zhang H, Long B, 2001. Roaring behavior of Hainan Eld's deer *Cervus eldi hainanus* male during the rut and its significance in reproduction. *Acta Zool. Sinica* 47: 481–487.