

“Harem defending” or “challenging”: alternative individual mating tactics in P^{ère} David's deer under different time constraint^{*}

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Abstract Three types of P^{ère} David's stags are distinguishable during the rutting season: the “harem masters”, “challengers” and “bachelors”. A “harem master” is a dominant stag that collects and controls the female deer. “Challengers” do not have a harem, they display at stands near the rut pond. When the hinds come out to feed, they may come to the stands to mate with the “challengers”, or the “challengers” may actively approach the hinds to seek the opportunity of mating. The “bachelors” do not rut during the reproductive season, they forage as usual in the non-breeding seasons, after foraging they sit in water. We were interested in which factor determines the rut tactics of individual stags. From the summer of 1996 to the summer of 1998, we conducted behavioral observations in the Beijing Milu Park to investigate the mechanism underlying the phenomenon. We found that the time budgets for life maintenance and rut are inversely related in the three types of stags. The time budgets for life maintenance and rut of the “harem masters”, “challengers” and “bachelors” were significantly different. The “harem masters” spent most of their time rutting and used little time for life maintenance activities such as feeding, rumination and drinking, they lived in a state of fasting, and depended on their body reserve to live during the rut. In contrast, “bachelors” invested most of their time feeding and resting but virtually no time rutting. The “challengers” had intermediate time budgets between those of harem masters and “bachelors”. Matings are skewed in proportion to the amount of time a stag invests in rut activities. However, while harem masters had higher probability of mating than those of “challengers” and “bachelors”, the difference in probability of mating between “challengers” and “bachelors” was not significant. The rut days of masters were significantly shorter than that of “challengers”, harem defending days of masters were significantly shorter than that of “challengers” whereas the post-rut recovery days of masters were significantly longer than that of the “challengers”. The results indicated that the rut is energy consuming in P^{ère} David's deer, the individual mating tactics are constrained by the available time and energy of stags [Acta Zoologica Sinica 50 (5): 706-713, 2004].

Key words P^{ère} David's deer, *Elaphurus davidianus*, Harem, Mating system, Harem masters, Challenger, Bachelor, Mating skew, Rut

“占群”还是“挑战”? 不同时间限制条件下麋鹿个体的交配计策^{*}

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摘要 在麋鹿的发情交配季节, 雄性麋鹿可区分为 3 种类型: “群主”、“挑战者”和“单身汉”。“群主”是一头圈占并控制雌鹿活动的优势雄性。“挑战者”不占有雌性繁殖群, 但在发情场附近地点展示炫耀。当雌性繁殖群的雌鹿外出采食靠近“挑战者”的展示炫耀地点时, “挑战者”会积极地寻求机会与之交配。“单身汉”在繁殖季节不表现发情行为。他们像非繁殖季节一样采食, 采食后蹲在水塘中休息。我们对何种因素决定麋鹿个体的发情交配计策感兴趣。1996 至 1998 年夏天, 我们在北京麋鹿苑观察麋鹿发情交配行为以分析导致这些行为差异的原因。结果发现, “群主”、“挑战者”和“单身汉”用于维持生命的时间预算与用于发情的时间预算成反比, 并且, “群主”、“挑战者”和“单身汉”用于维持生命的时间预算与用于发情的时间预算差异显著。“群主”

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的绝大部分时间用于发情占群, 而用于采食、饮水的时间很少, 所以, “群主”在发情期间基本上处于禁食状态, 靠消耗体内脂肪维持生命。“单身汉”则相反, 绝大部分时间用于采食、休息和反刍, 基本上没有发情行为。“挑战者”在发情行为与维持生命行为之间的时间则居于“群主”与“单身汉”之间。交配次数是偏态分布的, 与雄性发情时间呈正比。“群主”的交配概率最高, 而“挑战者”与“单身汉”之间交配概率差异不显著。但是, “群主”的发情时间却比“挑战者”显著短, 而“群主”发情后的恢复期却比“挑战者”显著长。这说明, 麋鹿发情是耗能的活动, 个体的交配计策受到雄性个体的可利用时间与能量的限制 [动物学报 50 (5): 706 - 713, 2004]。

关键词 麋鹿 繁殖群 交配制度 群主 挑战者 单身汉 交配偏倚 发情

In the process of mammalian reproduction, normally males perform an active role, presumably due to the lower cost of mating, for instance, relatively low cost of gametes production, large number of gametes available in males; males have a potential to fertilize many females. The reproductive potential of males is constrained only by male parental care and the spatial and temporal dispersion of female individuals (Davies, 1991). While monogamy is common among birds, polygamy dominates the mating systems of mammals, occurring in over 90% of the species (Clutton-Brock, 1989). Harem defending is common in cervids, but the rut strategy may vary in different populations within a single species. For example, both lekking and harem defending were reported in fallow deer *Dama dama* (Clutton-Brock, 1989; Clutton-Brock et al., 1982; Apollonio et al., 1990; Moore et al., 1995; Komers et al., 1997).

During the past two decades, researchers have discovered that within populations sexual behavior may vary in both sexes; thus the mating system of animals are now seen as the outcome of the reproductive strategy of individuals rather than as an evolved characteristics of species (Clutton-Brock, 1989; Davies, 1991; Gross, 1996; Taborsky, 1994; Field, 1992; Widemo and Sæther, 1999). There are individual variations in reproductive strategies and different individuals may have different mating tactics. In our study with the polygamous Père David's deer *Elaphurus davidianus*, even in an apparently harem defending population, the harem master can only control harems when the hinds are static. There are other stags that rut at individual stands, they display by bellowing, wallowing in mud, urine spraying, preorbital gland marking and adorning antlers with vines and grasses. The hinds may visit those stand holders and those stags then have chance of copulating with estrous hinds. However, we also notice that young stags less than three years old often do not participate in the rut. They feed, ruminate and rest as they did in the non-breeding seasons.

Péabon et al. (1999) showed that population density is important in shaping the lekking system in fallow deer. Although the population densities of Père David's deer in captivity are high (Jiang et al.,

2000), their mating system is predominately a harem system. What factor determines the rut tactics of individual stags in Père David's deer? Why don't all Père David's stags practice a single rut tactic? We investigated the time budgets and mating skew of individual Père David's stags during rut in relation to their age to test the hypothesis that rut tactics of individual stags are under different time constraints for reproduction.

1 Materials and methods

1.1 The Père David's deer

The Père David's deer was endemic to East Asia. The genus *Elaphurus* emerged in the Pleistocene and diversified during the Holocene. In the genus, there were other fossil species besides the *E. davidianus*, for example: *E. bifurcatus*, *E. chinanensis*, *E. lantianensis* and *E. formosanus* (Cao, 1992). However, as a victim of both habitat modification and over-hunting, all species of *Elaphurus* except *E. davidianus* died out, but the Père David's deer finally was extirpated in China around the turn of the 20th century. However, the Père David's deer was successfully bred in captivity in England and relocated to other parts of the world (Bedford, 1951 - 1952). The first conservation reintroduction of Père David's deer to China included two groups of 20 and 17 in 1985 and 1987, respectively. All 37 deer were donated by the Marquis of Tavistock of the Woburn Abbey and sponsored by the World Wildlife Fund (WWF, now the World Wide Fund for Nature) to be delivered to China. The deer were transported to the original site of the Nanyuan Royal Hunting Garden, where the last herd of Père David's deer lived in the 19th century, in the southern suburbs of Beijing. The Beijing Milu Park (39° 07' N, 116° 03' E) was created for the reintroduction, at a site that is located in the heart of the original Nanyuan Royal Hunting Garden. Another reintroduction of 39 Père David's deer was made to the Dafeng Natural Reserve in 1986. The reintroduced Père David's deer gradually acclimatized the local climate again (Jiang et al., 2000; Jiang et al., 2001). The annual life cycle of the Père David's deer in the Beijing Milu Park is shown in Table 1.

Table 1 The annual life cycle of Père David's deer in the Beijing Milu Park

Month	Grasses *	Stags	Hinds
January		Velvet antlers	Gestation
May	Grasses green up	Antler de-velvet and harden	Parturition and lactation
June	Leaves fully grown, vegetation in exuberance.	Start to chase and spur	Lactation and wean
July	Florescence	Rut	Estrous
September	Withering	Post-rut compensatory growth	Gestation
November		Shed hard antlers	Gestation

* : The growth of grasses may be postponed or advanced in condition to the available rainfall in spring.

Reproductive behaviors of Père David's deer stags show overt seasonal fluctuations, and the patterns of many seasonal reproductive behaviors strongly associated with testosterone secretion (Li et al., 2001, 2003, 2004). When Père David's deer stags rut, they display at wet muddy stands where they bellow, wallow in mud and toss turf with their antlers. They also adorn their antlers with green grass and vine, thus the size of their antlers look exaggerated with the long vines hanging on the antlers. Three types of Père David's stags are distinguishable during the rut season: the "harem master", the "challengers" and the "bachelors". A "harem master" is a dominant stag that controls the female deer at least when the females are static at rest in the "rut pond", a traditional place where a Père David's "harem master" holds the harem in consecutive years. The rut pond is created by tamping of the stags and hinds during rut, it is a barren and muddy pit, full of the smell of the urine sprayed by the harem master. While the harem members are at rest and regurgitated and ruminated their cuds, the harem master is in a state of excitation. It strolls around the rut pond, patrols and guides the harem, bellows and chases potential intruders. "Harem master" even try to herd the females while the latter are grazing and moving. But herding attempts by the harem master usually are unsuccessful during those periods, particularly when the harem is large. The harem members may act at their wills and interact with "challengers". Normally, the "challengers" do not have a harem. When they come out to feed, the hinds may come to the stands to mate with the "challengers", or the "challengers" may actively approach the hinds to seek opportunity of mating. When a "harem master" is exhausted during the prolonged rut, "challengers" may challenge the "harem master" and try to gain the control of the harem. A new "harem master" will then replace an exhausted "harem master". The succession of "harem masters" will continue until the end of rut. When the "harem master" is exhausted, several

"challengers" will compete for mates, thus the harem may be divided into several groups temporarily, each headed by a master stag. Such a phenomenon is more likely at the end of the rut season. The "bachelors" show little indication of rut activities during the reproductive season. They do not participate the rut but feed and sit in water most of time during the hot summer.

1.2 The hypothesis

Why are there three types of stags during rut? Animals allocate their time and energy to two major categories of activities: life maintenance (including growth) and reproduction, as the amount of time available for reproduction is related to age and the individual status (Bronson, 1989). Père David's deer practices an age dependent rut strategy (Jiang, 1999a). The "harem masters" are mainly stags of five-year-old or older, the "challengers" are mainly stags between 3 to 5-year-old, while the "bachelors" are mainly yearlings. Presumably, a stag's reproductive status is mainly constrained by time and energy available for the rut. The young stags invest little time in rutting, but the amount of time invested increases as age increases, stags will then become "challengers", and some of those stags may become the dominant ones and finally gain control of a harem. However, some of the stags may end up in the status of challenger during their lifespan. As the total amount of time available for either life maintenance or reproduction is limited, we predict that the time budgets for life maintaining and reproduction in "bachelors" and "harem masters" are inversely related, the "bachelors" will invest most of their time for life maintenance while the "harem masters" will devote most of their time to rutting. The "challengers" will have an intermediate type of time budget.

1.3 Study area

We conducted our study at the Beijing Milu Park. The area of the park is 60 ha and is located south of Beijing. About two thirds of parkland are used for holding the Père David's deer. The land-

scape used to be a wetland dominated by reed *Phragmites australis*. In the early 1990s, as results of both the grazing by the growing Père David's deer population and climate change, the land lost its original wetland appearance, and most of park vegetation is now dominated by grasses, such as goosegrass *Eleusine indica*, stinkgrass *Eragrostis cilianensis*, common crabgrass *Digitaria sanguinalis*, and green bristlegrass *Setaria viridis*. Where the grasses are overgrazed, roxburgh amaranth *Amaranthus roxburghianus* dominates the vegetation. Inside the park there are two large ponds, which provide the Père David's deer with rest sites during summer. The rut pond is near one of the ponds. There are also artificial grasslands in the park. The grasses are harvested and air dried in fall and used as supplementary hay for the Père David's deer during the winter. Annual average temperature is 13.1 °C, with mean temperatures of -3.4 °C in January and 26.4 °C in July. Average precipitation is about 60 cm. About 86% of the precipitation occurs in June-September. In some years, spring drought retards growth of grasses. In the Beijing Milu Park, deer graze on natural vegetation from July to September whereas from October to June they receive supplementary feed. There were 57 hinds, 31 stags and 42 fawns and yearlings in the reproductive herd in 1997 and 83 hinds, 48 stags and 28 fawns and yearlings in 1998. Calves were weighed, sex-determined and ear-tagged after birth.

1.4 Observation

Preliminary observations began in 1995 but the study was carried out from 1996 to 1998. During the breeding season, we checked the rut status of individual stags daily in the morning (8:00 - 9:00), noon (13:00 - 14:00) and evening (18:00 - 19:00). The number of "bachelors", "challengers", and the behavioral status of harem master were recorded. We recorded the days in rut and the recovery days after rut of the "harem masters" and "challengers". We also conducted dusk to dawn behavioral scans on the "harem masters", and selected "challengers" and "bachelors" (Martin and Bateson, 1993; Lehner, 1996). During three years of study, we scanned a total of 41 stags, with 2, 2, 5 "harem masters", 6, 6, 5 "challengers", and 6, 6, 5 "bachelors" in 1996, 1997 and 1998, respectively. The total amount of field observations was 1 971 hours. The scans were carried out at 3 minutes intervals. Twenty-one behaviors were recorded with a SJ-1 Event Recorder (Jiang, 1999b). Mating in Père David's deer is brief, only lasting for a few seconds, sometimes, it was difficult to distinguish mating from mounting, thus we pooled the mating and mounting as one behavioral category in the analyses. All behaviors were pooled into three main types:

maintenance, rut and others (Table 2). Within each major behavioral type, the behaviors may not be mutually exclusive, for example, rumination may occur when the Père David's deer are sitting, lying or standing in water. In such cases, we recorded the behaviors as sitting, lying and standing if the deer did not ruminate while sitting, lying and standing, and we recorded the behaviors as ruminating if the deer ruminated while sitting, lying and standing. However, the behaviors between the three major behavioral types, maintenance, rut and other behaviors, were mutually exclusive.

Table 2 Behaviours recorded during behavioural scans

Maintenance	Rut	Others
Foraging	Chasing	Walking
Drinking	Wallowing in mud	Standing
Urinating	Tossing turf with antler	Running
Defecating	Mounting	
Sitting/ standing in water	Copulating	
Sitting	Bellowing	
Lying	Antler adorning	
Ruminating	Sniffing the anogenital region of female	
	Herding hinds	
	Preorbital gland marking	

A total of 21 behaviors were recorded. The behaviors were grouped into three major categories.

1.5 Statistics

We used the Statistica™ to analyze the data. After the normality of data sets was checked, the Pearson Correlation was applied to calculate the correlations between the time for rut and time for maintenance, as well as the mating per unit time and the percentage of rut time in stags. The difference between the days of harem master holding a harem and days of "challengers" display was compared by the *t*-Test for independent samples. The one-way ANOVA was applied to analyze the variance among the time budgets and the mating and mounting per hour of the "harem masters", "challengers" and "bachelors". The LSD method was used to test for the significance of differences among the means. When $P < 0.05$, the difference was then taken as significantly different.

2 Results

2.1 Age and rut strategies

The Père David's stags shown an age dependent rut strategy. The stags aged five-year-old or older dominated the "harem masters", "challengers" were

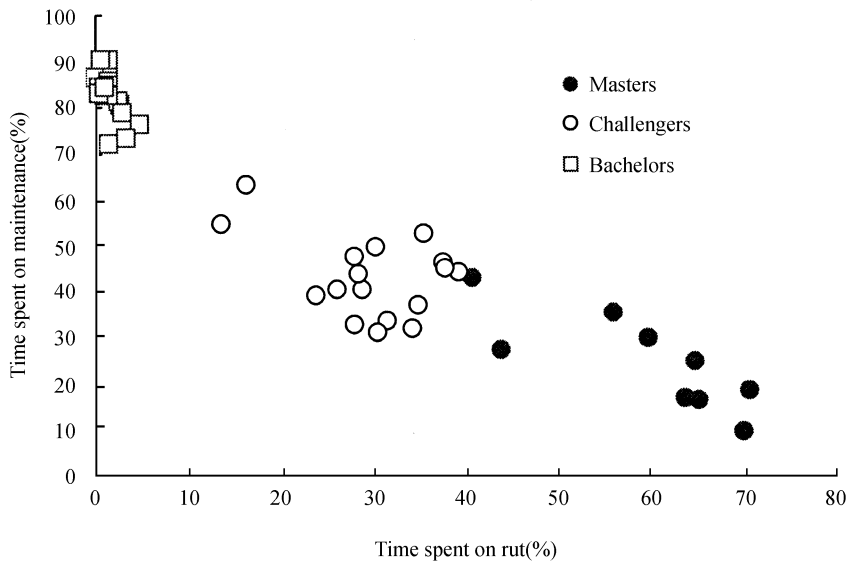


Fig. 1 Time budgets for maintenance and rut in "harem masters", "challengers" and "bachelors" of Père David's deer

three to five-years-old, whereas "bachelors" were mainly young stags less than three-year-old (Table 3).

Table 3 Number of "harem masters", "challengers" and "bachelors" recorded during 1996 - 1998

	Less than 3yr old	3 - 5yr old	> 5yr old
"Harem masters"	0	0	4
1996 "Challengers"	0	5	5
"Bachelors"	14	8	0
Total	14	13	9
"Harem masters"	0	0	4
1997 "Challengers"	0	5	2
"Bachelors"	14	6	0
Total	14	11	6
"Harem masters"	0	0	5
1998 "Challengers"	0	6	2
"Bachelors"	27	8	0
Total	27	14	7

2.2 Time budgets

The time budgets for life maintenance and rut were inversely related among stags ($r = -0.94$, $n = 49$, $P < 0.05$; Fig. 1). The time budgets for life maintenance and rutting of the "harem masters", "challengers" and "bachelors" were significantly different ($F_{2,38} = 233.08$, $P < 0.05$). The "harem masters" spent most of their time rutting and used little for life maintenance activities such as feeding, rumination and drinking. In contrast, the "bachelors" used most of their time to feed and rest but virtually

no time to rut. The "challengers" had an intermediate time budget between those of "harem masters" and "bachelors".

2.3 Mating skew

As the amount of time the stags invested in rutting increased, the opportunity of mating or mounting increased (Fig. 2). Mating differed significantly among the "harem masters", "challengers" and "bachelors" ($F_{2,38} = 30.02$, $P < 0.005$). However, while the masters had higher mating chances than those of "challengers" (LSD, $P < 0.05$) and "bachelors" (LSD, $P < 0.05$), the probability of mating were not significant different between "challengers" and "bachelors" (LSD, *NS*). The mating skew was obvious; the "harem masters" had about three-time higher probability of the mating than did the "challengers" (Fig. 3).

The total numbers of rut days of masters were significantly fewer than that of "challengers" ($t_{27} = 2.32$, $P < 0.05$, Fig. 4). Harem defending days of masters were significantly fewer than that of "challengers" ($t_{27} = 2.91$, $P < 0.05$) whereas the post-rut recovery period of masters was significantly longer than that of the "challengers" ($t_{27} = 13.79$, $P < 0.05$).

3 Discussion

We have illustrated that "challenger" may be an alternative individual tactic in mixed rut tactic set. Gosling and Petrie (1990) attribute the lek system in topi *Damaliscus lunatus* as a consequence of satellite behavior by small male topis at hotspots. In their study, the lekking strategy is an alternative strategy that is practiced by inferior males. In Père David's deer, harem defending and challenger tactic can also

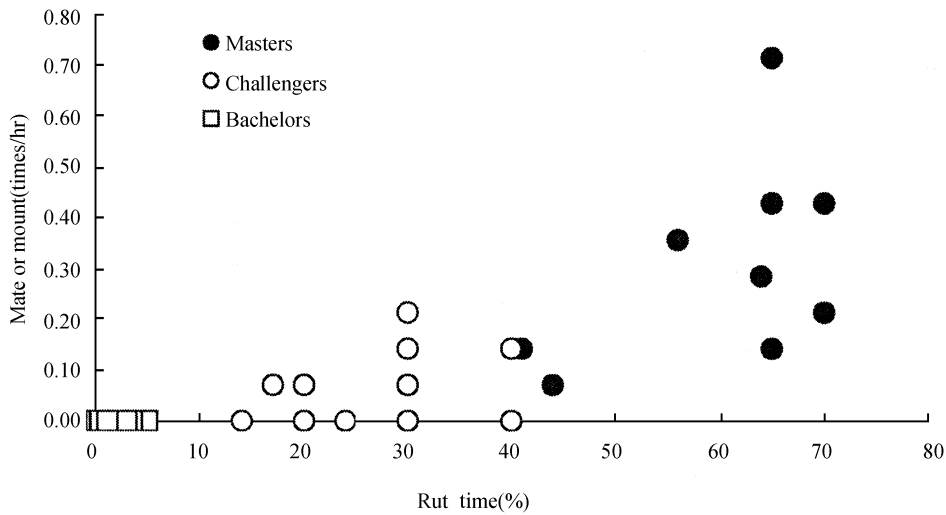


Fig. 2 Mating or mounting increased as the amount time of rut increased from “ bachelors ” to “ challengers ” to “ harem masters ” in the Père David's deer

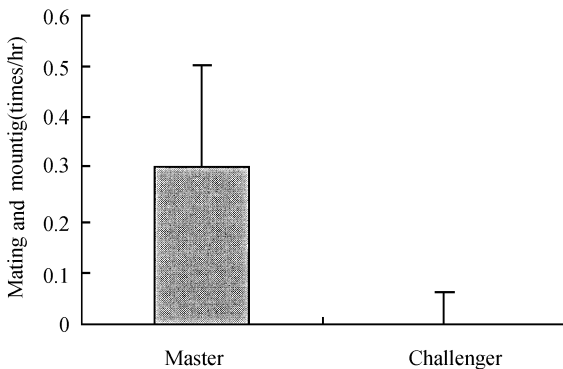


Fig. 3 Mating skew in the Père David's deer
The “ harem masters ” had higher mating rate than that of “ challengers ”.

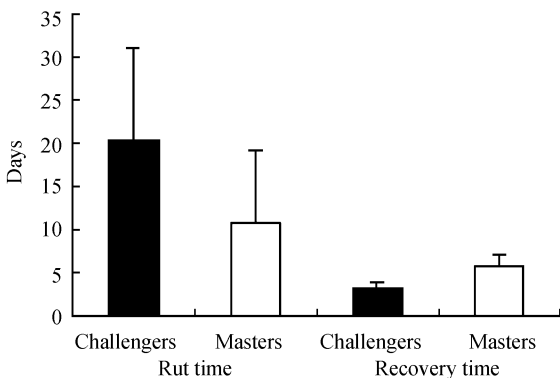


Fig. 4 Rut time and recovery time in the “ harem masters ” and “ challengers ”
The “ harem masters ” had shorter rut that that of “ challengers ” but a longer recovery time than that of “ challengers ”. Recovery time is defined as days from the time a “ harem master ” is expelled from the rut pond and sits on ground until he fully recovers from the fatigue , foraging and moving like other stags again.

cease ingestion of food and even to cease drinking (Bedford , 1951 - 1952) , and live on their body reserves. Thus the harem holders need a longer period of recovery after the exhaustion of a rut. The “ challengers ”, on the other hand, display at the stands they rut longer than the “ harem masters ” who guide the harem. But the “ challenger ” strategists have less chances of mating. Balancing the reproductive benefit and cost , individual Père David's stag may choose one of the mating strategies.

An optimal age at first reproduction evolves where the benefits of reproduction outweigh the costs. Only when a stag is fully developed in body size, can he match the campaign for a harem in the Père David's deer. Komers et al. (1997) found that dominance rank was the strongest factor affecting the reproductive behavior of male fallow deer , but high dominance rank confers a high benefit for males of all age (Apollonio et al. , 1992 ; Clutton-Brock et al. , 1988) . Dominance in the Père David's deer is age-related, the stags only adopt the harem defending strategy when they reach maturation.

The behavioral time budgets for the “ harem masters ”, “ challengers ” and “ bachelors ” indicated that the three tactics are time constrained during the rut. As the young stags, have not yet fully developed, they have to devote their time to feeding. They adopt a sit and wait strategy for future reproductive opportunities. The “ challengers ” practice a satellite rut tactic; they clump around the “ rut ” pond, which is held by the harem master with his hinds. By displaying to attract hinds in estrous and sometimes coerce them to mate , a “ challenger ” had marginal mating opportunities. However, “ challengers ” have two additional advantages: first , when the “ harem master ” is exhausted, the “ challengers ”

be treated as alternative strategies. While the harem holders have more chances of mating, they have to

will evict the "harem master" and replace him. Second, the "challengers" practice the skill of reproduction. If a "challenger" rush and compete for control of the harem, he will face fierce fights, which presumably will end up with severe wounds or even death in escalated contests. A "harem master" with its rank and fully developed body can sustain a period without much feeding. It thus can devote more time in guiding females and evicting intruders from the rut pond.

Cant and Johnstone (1999) presented a model to explain the incentive of a dominant male to allow subordinate individuals to breed. Presumably, the cluster of "challengers" around the harem in the rut pond may stimulate hinds coming to estrous, therefore, the harem master may tolerate the display of the "challengers", provided the "challengers" do not approach the hinds in his harem. To evict the "challengers" may be energetically too expensive or impossible for the harem master.

The age specific rut tactics may be a mechanism to avoid inbreeding. The Père David's deer was artificially propagated in captivity with a founder population of 18 individuals, where only 11 of the 18 founders were capable of breeding (Bedford, 1951 - 1952). Nevertheless, the Père David's deer survived the bottleneck and its population number increased. Beck and Wemmer (1983) pointed out the Père David's deer is one of the few species of large mammals that are extinct in the wild but safely preserved in captivity. When the Père David's deer were relocated to other sites from the Woburn Abbey, the populations of relocation were all of small size. For example the reintroductions made to China were of 35 and 37 individual deer. Up to now, both the reintroduced populations have grown, and no severe signs of inbreeding have been found (Jiang et al., 2000). Recently, a group of Père David's deer was released into the field (Hu and Jiang, 2002). One puzzle is how did the deer survive the heavy inbreeding? The age specific rut strategy avoids the most possible and the worst case of inbreeding in small populations: father-daughter mating. Mating success in deer is high during the middle age of their lifespan, for example, fallow deer had high mating rate between the ages of five to eight years (McElligott and Hayden, 2000). In such an age dependent mating system, when daughters have reached paternal age of full reproduction, their fathers have already passed their age of peak reproductive performance.

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