2002

# Anti-predation does not fully explain grouping in the Chinese water deer (Hydropotes Inermis)

Lixing Sun
*Central Washington University*, lixing@cwu.edu



Recommended Citation
Sun, L. (2002). Anti-predation does not fully explain grouping in the Chinese water deer (*Hydropotes inermis*). *Acta Zoologica Sinica, 48*(3), 201-10.

动物学报 **48**(3) :302～308 , 2002
*Acta Zoologica Sinica*

# ANTI-PREDATION DOES NOT FULLY EXPLAIN GROUPING IN THE CHINESE WATER DEER ( HYDROPOTES INERMIS)

SUN Li-Xing
*( Department of Biological Sciences , Central Washington University , Ellensburg , WA* 98926-7537 , *USA)*

**Abstract** The grouping behavior of the Chinese water deer *( Hydropotes inermis)* was studied at Poyang Lake National Nature Reserve , Jiangxi , China. I made three predictions to test the hypothesis that grouping is an anti-predatory strategy: (1) group size is negatively related to vegetation cover , (2) animals in groups have more time to feed than solitary animals , and (3) animals spend less time in vigilance when they are in groups than when they are alone. Results showed that group size was largest in the mating season and smallest in the parturition season. Deer tended to form larger groups when they were in short grass areas than in tall grass areas. Hence , the first prediction is supported. However , solitary deer and deer in groups did not differ in time allocated to feeding or vigilance. Therefore , predictions 2 and 3 are not supported. Time budget analysis revealed that females with young allocated less time to feeding , but more time to walking during the non-mating season. During the mating season , females grouped with males spent less time feeding than solitary females , and solitary males spent more time looking for females than did males grouped with females during the mating season. In light of the complications found in the grouping behavior of the water deer , the anti-predatory hypothesis seems to be insufficient as the only reason for the deer to group. Other socio-ecological factors are also important in determining the grouping behavior of this species.

**Key words** Water deer *( Hydropotes inermis)* , Grouping behavior , Anti-predation , Group size , Time-budget

Social grouping is intensively studied in ungulates , especially in relation to foraging and predation (reviewed by Kie , 1999). One exciting recent development is that the social grouping behavior has been reported in several rare Chinese ungulate species (Jiang *et al*. , 2000; Lei *et al*. , 2001a , b). Grouping behavior in ungulates can be affected by a variety of socio-ecological factors (e. g. Jarman , 1974; Wilson , 1975; Clutton-Brock *et al*. , 1982). The effect of vegetation cover on group size , however , has been most intensively studied since Dasmann and Taber (1956) first observed the negative association between vegetation cover and group size. This finding has later been substantiated and suggested as an anti-predatory strategy (e. g. Franklin *et al*. , 1975; Hardin *et al*. , 1976; Hirth , 1977; Miura , 1983). This is because animals in large groups , comparing with those in small groups or solitary individuals , are more likely to detect approaching predators early because only some individuals need to be vigilant at any specific time and others , therefore , can channel more time to engage in other important activities such as feeding. Studies examining this hypothesis as those cited above are typically carried out by comparing several populations or local demes in different habitats (e. g. Hirth , 1977). There is one obvious weakness in this approach: it may not allow us to separate the confounding factor that these populations or demes may have different behavioral adaptations to their respective habitats. As such , studies of grouping behavior of the same individuals in different habitats , such as that by Molvar and Bowyer (1994) , will allow us to tease apart the interaction between behavior and habitat , and provide a stronger test for the anti-predatory hypothesis. Thus , I attempted an investigation on this issue in the Chinese water deer *( Hydropotes inermis)* .

The Chinese water deer is a small , territorial species (Stadler , 1991; Sun and Xiao , 1995).

Received 11 March , 2001; revised 20 November , 2001

**Brief introduction to the first author** Lixing Sun , 37 , Associate Professor of Biology. Research interests: evolution and ecology of vertebrate communication systems , social evolution. E-mail: lixing@cwu. edu

During the mating season, males occupy a small territory on feeding ground preferred by females. Females' feeding time (active period) during the daytime is early morning and late afternoon. Between the two feeding periods, females vacate males' territories and ruminate and rest on open areas (resting period). Males may leave their territories to follow females (Sun and Xiao, 1995). Males typically avoid other males, whereas females often form small, loose aggregations (Sun and Dai, 1995). In this paper, while presenting the seasonal variation in grouping pattern, I examined the anti-predatory hypothesis using a population of the Chinese water deer under several social and habitat conditions. I specifically tested three predictions derived from the anti-predatory hypothesis: (1) group size should be larger when vegetation cover is low than when vegetation cover is high, (2) animals should spend more time feeding when they are in groups than when they are alone, and (3) animals in groups should allocate less time to vigilance than solitary individuals.

## 1 Study Area and Methods

I conducted the study at Poyang Lake National Nature Reserve, Yongxiu County, Jiangxi, China from 1988 to 1989. The habitat of the water deer is the vast grasslands at the mouth of the Ganjiang River (see Sun and Xiao, 1995 for map). Most of those grasslands are submerged for several weeks between May and August every year when the water in the Changjiang River is impounded into the lake. The deer take shelter in nearby hills during this time and return to the grasslands after the water retreats. Because there are numerous small pockets of suitable habitats in these hills, the deer are never forced to form any large congregations as a result of lack of open grassland. Grasses grow back after water retreats, providing the deer with bountiful food and shelter. However, local farmers clear-cut almost all the grasses between late October and early November, which is the beginning of the mating season of the deer. Grass-cutting, though extensive, is concentrated in small areas each day and therefore, few deer are affected at one time. The mating season lasts two and a half months. During this period the habitat is largely open except for a few patches of tall grass areas. More details about the habitat can be found elsewhere (Sun *et al.*, 1994; Sun and Dai, 1995; Sun and Xiao, 1995).

From May 1988 to January 1989, I counted the number of deer in each group. A group here is operationally defined as a gathering of animals with the maximal inter-individual distance less than 20 m and showing coordinate behavior (see also Clutton-Brock *et al.*, 1982). This definition of group does not require a relative stable relationship: it is a convenient way to describe spatial proximity among conspecific individuals.

A walking or standing adult deer, because of its size, can be easily seen in areas with grass height lower than 30 cm, although it is not so conspicuous if the average grass height is higher than 30 cm. I thus dichotomized the habitat as tall-grass areas where the height of grass was over 30 cm, and short-grass areas where the height of grass was below 30 cm for the entire study period. To avoid underestimating group size in tall grass areas because of poor visibility, I counted the number of individuals in the vicinity numerous times to ascertain all individuals were included. Fortunately, because the group size is characteristically small, it was unlikely to miscount deer in a group in practice.

A year was divided into the mating season from the end of October until mid-January, and the non-mating season (remaining months). The latter was further divided into the parturition season (May and June) and the non-breeding season (remaining months). I used a pair of 10 ×7 binoculars and a 10 × 30 Nikon spotting scope for observation. I discriminated between males and females by presence or absence of tusks. Yearling males without apparent tusks were recognized by their male-specific behavior during the mating season. Cassette-tape recorders were used to aid in recording behavior of the deer. The behavioral patterns and their respective durations were then transcribed onto notebooks. Since it was difficult to find and observe a deer in thick and tall

grasses, the sample sizes were relatively small except for the mating season, when the land was open after the grasses were cut. I used the continuous recording method (Altmann, 1974; Martin *et al.*, 1986) whenever possible to monitor the behavior of the deer and obtained approximately 30 hours of tape recorded in the entire study. No observation was made during grass-cutting time because of possible disturbance to the normal behavior of the deer.

The behavioral patterns of the deer in activity were categorized into feeding, looking, walking and others. The last category included all the infrequent behaviors such as grooming, defecation, urination, marking and social interactions. Resting-rumination and sleeping during inactive period were not included in the analysis. For comparisons of group size in different seasons, I used a parametric Z-test because the sample size was large ($n > 100$). To compare the difference in the proportion of solitary individuals versus individuals in groups, I used the non-parametric $\chi^2$-test. For all the time-budget data, I first calculated the percentage of each behavior in an activity bout and then normalized the data by arcsine transformation before performing a $t$-test for small sample sizes ($n < 100$). For all parametric tests, the normality and equal variance prerequisites had been tested and meet before performing the tests. All statistical tests were two-tailed with $\alpha = 0.05$ as the significance level, and the data were expressed as mean $\pm SE$.

## 2 Results

Regardless of the vegetation height, the group size of the water deer in the study area was 1.40 ± 0.22 ($SE$) ($n$ = 1 326 sightings) with the smallest in May to July and the largest in November (Fig. 1). The group size in the non-mating season (May to September) was 1.21 ±0.01 ($n$ = 124 sightings; range: 1 - 4), significantly different from that in the mating season (1.64 ±0.08; $n$ = 1080 sightings; range: 1 - 7; $Z = 9.326$, $P < 0.001$). The percentage of solitary individuals in different periods decreased from the parturition season through non-breeding and mating seasons, whereas that of individuals in groups increased (Table 1). During the mating season, 69.90 % of identifiable solitary individuals were males, significantly more than that of solitary females (30.10 %) ($\chi^2 = 22.57$, $df = 1$, $P < 0.001$). The most frequently observed type of group during this season consisted of a male and a female (58 % of all groups). In all observed groups, 90 % were composed of two or three individuals while only 10 % had more than three individuals. I never observed two males in the same group.

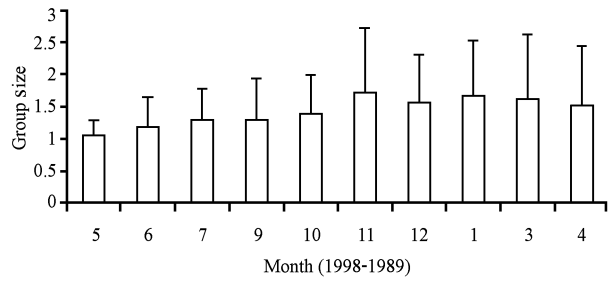


**Fig. 1 Changes of group size over time**

Error bars are standard deviations

During the mating season, group size in the tall grass area (1.49 ±0.03, $n$ = 567 sightings) was significantly smaller than that in the short grass area (1.79 ±0.04, $n$ = 551 sightings) ($Z = 5.779$, $P < 0.001$). This supports the first prediction. However, no significant differences were detected in group size between active period and resting period of the day, nor in the ratio of solitary versus grouped individuals between the two periods.

The time-budget of females during the non-mating season is shown in Fig. 2. There was no significant difference between solitary females and females grouped with males in the four behavioral categories. The only difference was that females with young spent significantly less time feeding but more time walking than that of solitary females (for feeding: $t = 2.57$, $df = 14$, $P = 0.022$; for walking: $t = 2.75$, $df = 14$, $P = 0.016$) and females grouped with males (for feeding: $t = 2.95$, $df = 8$, $P = 0.018$; for walking: $t = 2.96$, $df = 8$, $P = 0.018$). The time-budget of males during the non-mating season is shown in Fig. 3. There is no significant difference in any behavioral categories for solitary males and males grouped with females.

**Table 1 Group size of water deer in different seasons**

| | | Group size | | | | | | | | Sample size (Number of sightings) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Range | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| Parturition season | Number of groups | 1 - 3 | 60 | 9 | 1 | | | | | 70 |
| (May and June) | % | | 85.71 | 12.86 | 1.43 | | | | | |
| | Number of individuals | | 60 | 18 | 3 | | | | | 81 |
| | % | | 74.07 | 22.22 | 3.7 | | | | | |
| Non-breeding season | Number of groups | 1 - 4 | 44 | 7 | 1 | 1 | | | | 53 |
| (February to April and | % | | 83.02 | 13.21 | 1.89 | 1.89 | | | | |
| July to September) | Number of individuals | | 44 | 14 | 3 | 4 | | | | 69 |
| | % | | 63.77 | 20.29 | 4.35 | 5.8 | | | | |
| Mating season | Number of groups | 1 - 7 | 594 | 345 | 100 | 29 | 5 | 5 | 2 | 1 080 |
| (November to January) | % | | 50 | 31.94 | 9.26 | 2.69 | 0.46 | 0.46 | 0.19 | |
| | Number of individuals | | 594 | 690 | 300 | 116 | 25 | 30 | 14 | 1 769 |
| | % | | 33.58 | 39.01 | 16.96 | 6.56 | 1.41 | 1.7 | 0.79 | |

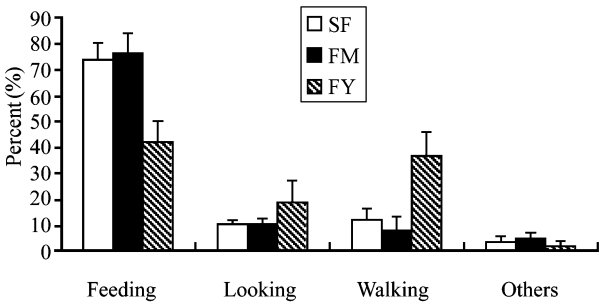


**Fig. 2 Time budget of females when in activity during the non-mating season**

SF: single females FM: females associated with males FY: females with the young Bars are standard errors

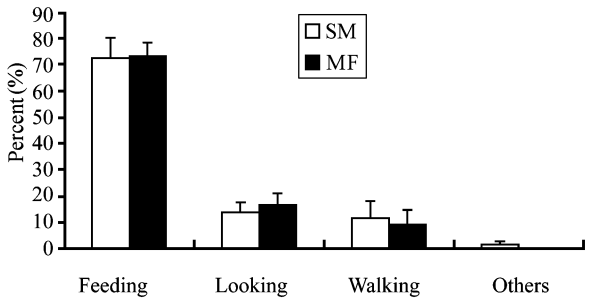


**Fig. 3 Time budget of males when in activity during the non-mating season**

SM: single males MF: males associated with females Bars are standard errors

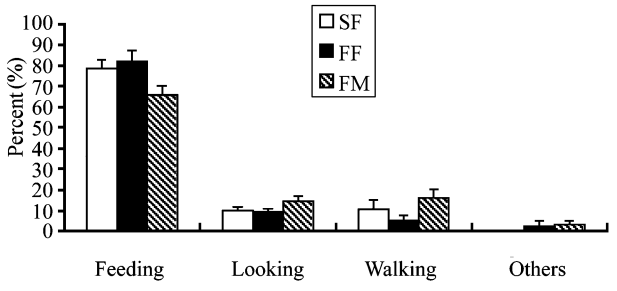


**Fig. 4 Time budget of females when in activity during the mating season**

SF: single females FF: females associated with females FM: females associated with males Bars are standard errors

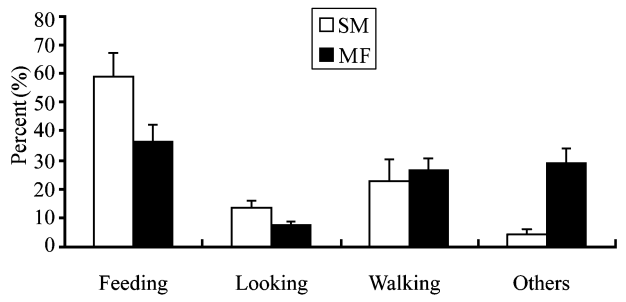


**Fig. 5 Time budget of males when in activity during the mating season**

SM: single males MF: males associated with females Bars are standard errors

The time-budget of females during the mating season is shown in Fig. 4. Single females and females grouped with other females allocated statistically equal amounts of time to the four behavioral categories. Females grouped with males, however, spent less time feeding than solitary females ($t = 2.11$, $df = 27$, $P = 0.044$) and females grouped with other females ($t = 2.22$, $df = 20$, $P = 0.039$). The time-budget of males during the mating season is shown in Fig. 5. Single males allocated more time to looking around ($t = 2.41$, $df = 38$, $P = 0.021$) and less time to other behaviors ($t = 2.88$, $df = 38$, $P =$

*0.007)* than males grouped with females. Single males tended to spend more time feeding than males grouped with females, but the difference was marginally non-significant ( $t = 1.99$, $df = 38$, $P = 0.054$). These results fail to support the second and third prediction.

## 3 Discussion

The group size of the water deer in my study area was 1.40 on average, slightly larger than that in the introduced population in Britain (1.28) (Cooke *et al.*, 1981, 1983). It is almost the same as that of the Indian muntjac *(Muntiacus muntjak)* (1.41) (Barrette, 1977) but larger than that of the musk deer *(Muschus chrysogaster)* (1.01) (Green, 1987) and the spotted chevrotain *(Tragulus meminna)* (1.0) (Eisenberg *et al.*, 1972). I lack the data from February, March, April and August, which would likely make the mean of the group size slightly larger.

The reason why the group size fell into the lowest point in the parturition season was that each female actively sought a quiet location to give birth and care for her fawns. Males that used to be grouped with all-female groups became solitary, too. As fawns grew and could follow their mothers, females with fawns could group with other deer and consequently, the overall group size rose again. The main reason for large group size during the mating season was that males actively associated themselves with females, seeking for mating opportunities. Males disassociated themselves from females during the non-mating season due to lack of mating opportunities, resulting in a high proportion of solitary individuals (Table 1) and thus, smaller average group size.

My study showed that group size was larger when deer were in short grass areas than when they were in tall grass areas. This supports the first prediction by the anti-predatory hypothesis. Allocation of time to different behaviors was affected by the interaction among group members. During the non-mating season, my results showed that the effect of this interaction was not salient in either males or females, but it was for females with young. Females with fawns devoted more time to walking at the sacrifice of some feeding time so as to care for young. Interestingly, females with fawns did not spend more time looking around for predators than did females without fawns, contrary to findings in Whipsnade Park, England (Zhang, 1996). Perhaps, these females may also be paying attention to predators while they were walking.

The effect of interaction among group members became significant with the presence of males during the mating season. It appears that the presence of males had a negative effect on the feeding time of females in this study. Males actively pursue females during the mating season, especially within their territories, which are also females' prime feeding sites (Sun and Dai, 1995; Sun and Xiao, 1995). Females' feeding was often disrupted due to unwanted courtship from males. This may be the reason why solitary females could allocate more time to feeding than did females grouped with males. Comparing with males in groups, solitary males had to allocate more time to looking around for the presence of females or for the invasion of other males into their territories. Therefore, solitary males allocated more time to looking or marking (in the form of stem-rubbing, urination or defecation, see Sun *et al.*, 1994) within their territories. They could also spend more time feeding in their territories when no females or potential male invaders were nearby. However, once males were grouped with females, males showed more interest in pursuing females. This included following and courting females (Sun, 1989), resulting in a lowered proportion of feeding time. Thus, time-budget analysis showed there was a cost of grouping in terms of feeding efficiency during the mating season.

Historically, there were many sympatric predators preying on water deer, including tigers *(Panthera tigris)*, leopards *(P. pardus)* and red dogs *(Cuon alpinus)*. Currently, domestic dogs are

* SUN, L. 1989 The social behavior and organization of the Chinese water deer. MS thesis. East China Normal University.

the main predator of the deer: about 5 % - 10 % of adult water deer and a much higher proportion of fawns were killed by dogs (Sun, unpublished data). Although dogs are not water deer's natural predator, the way they prey on deer is not fundamentally different. As such, it is unlikely that water deer's antipredatory response to dogs would be different from that to its historical predators. Because grouping can reduce the rate of being preyed upon, the hypothesis of grouping as an anti-predatory strategy predicts that solitary individuals should be few and that grouping could increase feeding efficiency by lowering the time allocated to vigilance for each individual in the group. However, since there were a substantial number of solitary individuals present during the non-mating season (Table 1) and no evidence from my study showed that deer in groups spent less time looking around, the grouping behavior in water deer can not be fully explained by the anti-predatory hypothesis. Other socio-ecological factors are also important in determining the grouping behavior of the deer.

One such factor could be the differential reproductive strategies in males and females. In a species like the water deer where males do not contribute anything but gametes, males are more strongly selected for obtaining mating opportunities than females, whereas females are more strongly selected for improving feeding efficiency (Bateman, 1948; Trivers, 1972). In my study area, although there was some excess of females (Sun, 1989), the competition among males for access to females was intense during the mating season (Sun and Dai, 1995; Sun and Xiao, 1995). Since only one male could be present in a group, and males were constantly attempting to associate themselves with females (Sun and Dai, 1995), more solitary males than solitary females were observed during the mating season. Males in general spent less time feeding so that more time could be channeled to behaviors directly related to gaining mating opportunities, such as marking territories, and following and courting females (Sun, 1989; Sun *et al.*, 1994). Additionally, time-budgeting in males was dependent on whether they were solitary or were grouped with females. Female deer, however, may have maintained a similar feeding efficiency during the mating season as that in other seasons. While females grouped with males may reduce their food intake rate, they may get access to better feeding grounds occupied by males. In this scenario, the argument that grouping is an anti-predatory strategy is obviously not suitable. Rather, males and females group for different reasons, reflecting differences in their strategies of gaining reproductive success. This has been demonstrated in the milu, *Elaphurus davidianus* (Jiang *et al.*, 2000). Thus, I conclude that grouping for the reason of anti-predation is an oversimplification and can not be used to fully explain grouping behavior in the water deer. More research is needed to uncover other socio-ecological factors important for the grouping behavior.

**Acknowledgements** I thank H. Lu, B. Xiao, E. Zhang and L. Zhu for their assistance and encouragement during my study. I am also grateful to Z. Huang, X. Song and B. Xiao who helped in my field work. D. Moore, C. Straub and two anonymous reviewers provided many good comments for the improvement of the manuscript.

## References

Altmann, J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**: 227～265.

Barrette, C. 1977 Some aspects of the behaviour of munjacs in Wilpattu National Park. *Mammalia* **41**: 1～34.

Bateman, A. J. 1948 Intra-sexual selection in *Drosophila*. *Heredity* **2**: 349～368.

Clutton-Brock, T. H., F. E. Guinness and S. D. Albon 1982 Red Deer: Behaviour and Ecology of Two Sexes. Chicago: Chicago University Press.

Cooke, A. S. and L. Farrell 1981 The ecology of Chinese water deer (*Hydropotes inermis*) on Woodwalton Fen Nature Reserve. Huntington: Nature Conservancy Council.

Cooke, A. S. and L. Farrell 1983 Chinese water deer (*Hydropotes inermis*). British Deer Society Publication No. 2. Canterbury: Elvy and

Gibbs.

Dasmann, R. F. and R. D. Taber 1956 Behavior of Columbian black-tailed deer with reference to population ecology. *J. Mammal.* **37**: 143～164.

Eisenberg, J. F. and M. Lockhart 1972 An ecological reconnaissance of Wilpattu National Park, Ceylon. *Smithon. Contr. Zool.* **101**: 1～118.

Franklin, W. W., A. S. Mossan and M. Dole 1975 Social organization and home range of Roosevelt elk. *J. Mammal.* **56**: 102～118.

Green, M. J. B. 1987 Scent-marking in the Himalayan musk deer (*Moschus chrysogaster*). *J. Zool., Lond.* **1**: 721～737.

Hardin, J. W., N. J. Silvy and W. D. Klimstra 1976 Group size and composition of the Florida key deer. *J. Wildl. Manage.* **40**: 454～463.

Hirth, D. H. 1977 Social behavior of white-tailed deer in relation to habitat. *Wildl. Monogr.* 53.

Jarman, P. J. 1974 The social organisation of antelope in relation to their ecology. *Behavior* **48**: 215～267.

Jiang, Z., B. Liu, Y. Yang, G. Han and H. Hu 2000 Attracted by the same sex, or repelled by the opposite sex? *Chinese Science Bulletin* **45**: 485～491.

Kie, J. G. 1999 Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *J. Mammal.* **80**: 1 114～1 129.

Lei, R., Z. Jiang and B. Liu. 2001 Group size and group composition in Przewalski's gazelle. *Folia Zool.* **50**: 117～126.

Lei, R., Z. Jiang and B. Liu 2001 Group pattern and social segregation in Przewalski's gazelle (*Procapra preswalskii*) around Qinghai Lake, China. *J. Zool., Lond.* **255**: 175～180.

Martin, P. and P. Bateson 1986 Measuring Behaviour: An Introductory Guide. Cambridge: Cambridge University.

Miura, S. 1984 Social behavior and territoriality in male sika deer (*Cervus nippon* Temminck, 1838) during the rut. *Z. Tierpsychol.* **64**: 33～73.

Molvar, E. M. and R. T. Bowyer 1994 Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *J. Mammal.* **75**: 621～630.

Stadler, S. 1991 Behaviour and social organisation of Chinese water deer (*Hydropotes inermis*) under semi-natural conditions. Ph. D. dissertation. Uiversität Bielefeld.

Sun, L. and N. Dai 1995 Male and female association and mating system in the Chinese water deer (*Hydropotes inermis*). *Mammalia* **59**: 171～178.

Sun, L. and B. Xiao 1995 The effect of female distribution on male territoriality in Chinese water deer (*Hydropotes inermis*). *Z. Säugetierk.* **60**: 33～40.

Sun, L., B. Xiao and N. Dai 1994 Scent marking behaviour in the male Chinese water deer. *Acta Theriol.* **39**: 177～184.

Wilson, E. O. 1975 Sociobiology: the New Synthesis. Cambridge: Harvard University Press.

Zhang, E. 1996 Behavioural Ecology of the Chinese Water Deer at Whipsnade Wild Animal Park, England. Ph. D. dissertation. Cambridge University.

## 中 文 摘 要

# 反捕食不能充分解释獐的集群行为

孙立新

(中华盛顿大学生物系 美国)

**我在江西鄱阳湖国家自然保护区研究了獐（*Hydropotes inermis*）的集群行为并检验了集群是动物反捕食对策的假说。如果这个假说成立，我们则可以做三个预测：(1) 集群大小应与植物覆盖度成负相关；(2) 集群动物比单独活动的动物有更多的时间取食；(3) 集群动物与单独活动的动物相比，用于警戒的时间较少。结果表明，獐的集群在交配季节最大而在产仔季节最小，獐在短草期比在高草期倾向于形成较大集群。因此，本研究支持了第一个预测。但是，集群的獐和单独活动的獐在取食和警戒时间分配上并无差异。因此，本研究不支持第二和第三个预测。时间收支（time budget）分析显示，在非交配季节，带幼仔的雌性用于取食的时间较少但走动频繁。在交配季节，与单独活动的雌性相比，与雄性在一起的雌性用于取食的时间较少，而单独活动的雄性却比与雌性在一起的雄性花较多的时间用于观望寻找雌性。鉴于獐集群行为的复杂性，本研究认为，獐并不只因反捕食而集群，其它社会和生态因子在决定獐的集群行为中也很重要。**

**关键词** 獐 集群行为 反捕食 集群大小 时间收支