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Mating Behaviors, Courtship Rank and Mating Success of Male Feral Cat (*Felis catus*)

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Abstract — The mating behavior of the male feral cat (*Felis catus*) living on a small island was investigated. The cats in the study area (6.0 ha) formed the "feeding groups" at the garbage sites (Yamane et al. 1994; Izawa et al. 1982). We examined the factors influencing fighting ability, rank during courtship, and mating success of the male cat. Males with heavier body weight mostly won over lighter males in the agonistic encounters during the estrous season. Heavier males occupied the more advantageous positions to copulate with the estrous females and had higher mating success. These results suggest that body weight was one of the important factors affecting the courtship rank and the mating success of the male cat. When males visited and courted the females of feeding groups other than their own, they were sometimes defeated by the lighter males in that particular group, which lowered their courtship rank and success in copulations. These results indicate that the location of the courting male (inside or outside of its own group) and the kind of females they courted (member of the same group or not) were also important factors.

Introduction

In polygynous or promiscuous mating systems, various types of severe male-male competition for mates are expected (Trivers 1972; Clutton-Brock 1989; Davies 1991). Several studies of these polygynous mammalian species have shown that the mating success of males was closely related to their fighting ability which depended on body size or age (e.g., red deer, *Cervus elaphus*: Clutton-Brock et al. 1982; African elephant, *Loxodonta africana*: Poole 1989; elephant seals, *Mirounga angustirostris*: Cox & Le Boeuf 1977).

The majority of species belonging to Felidae are solitary-living, and individuals are spatially scattered (Sandell 1989). This consequently results in a low level of male aggregation and competition for an estrous female. For this reason, little attention has so far been given to studies examining the factors that influence male fighting ability, social rank, and mating success. However, the social structures of the feral cats (*Felis catus*) are very flexible (Izawa et al. 1982; Izawa 1984; Liberg & Sandell 1988); ranging from solitary to group living. In the high density cat populations, severe competition among males for a receptive female is expected. Natoli & De Vito (1988, 1991) reported on the mating behaviors and male mating strategies of such cat populations, but could not determine what factors influenced the dominance rank and the mating success of the male. On the other hand, Liberg (1983) described the relationships between the dominance courtship rank and the body weight of males in a low density population, but the sample size in his study was too small to allow quantitative examination of the factors affecting their mating success.

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In this paper, we will describe the mating behaviors of the male feral cat living in a group of high population density, and examine how the body size and the age of the male influences fighting ability, rank during courtship, and mating success. We have used the male body weight as the index of male body size. The body weight of about 96% (46/48) of identified males were measured just before an estrous season. We will also examine how the location of the male (inside or outside their own feeding group) affects rank during courtship and mating success.

Study Area and Methods

This study was carried out at Ainoshima Island, which is located about 7 km off the cost of Shingu, in the Fukuoka Prefecture of Japan (Fig. 1). The size of the island is 125 ha, and about 90% of it is covered with bush. Around 500 people live on the island, and the majority of them make a living by fishing. The main study area (6.0 ha) is shown in Fig. 1. All cats in the main study area have been individually identified since 1989. Of 74 sexually matured cats in January 1993, 48 were male and 26 were female. In the study area, there were four garbage sites (A, B, C and D in Fig. 1), which provided the cat population with an abundance of food resource (Yamane et al. 1994). Because each cat utilized only one of the four garbage sites for feeding and resting, it was concluded that cat population on this island formed the "feeding group" (Yamane et al. 1994; Izawa et al. 1982; Izawa 1984). In 1991, two sib females from feeding group "C" moved to a newly established garbage site, and gave birth to kittens there. We regarded this new group as the fifth feeding group and named the feeding group, "E" (Fig. 1).

From 1989, we continued to survey the cats in the study area, at least 3 days each month, in order to identify the new-born kittens and their mother, the group that the cats belonged to, and deaths of cat. By the spring of 1993, the age of all cats less than 5 years old were documented. The male cats were weighed in January, 1993, just before their rutting period

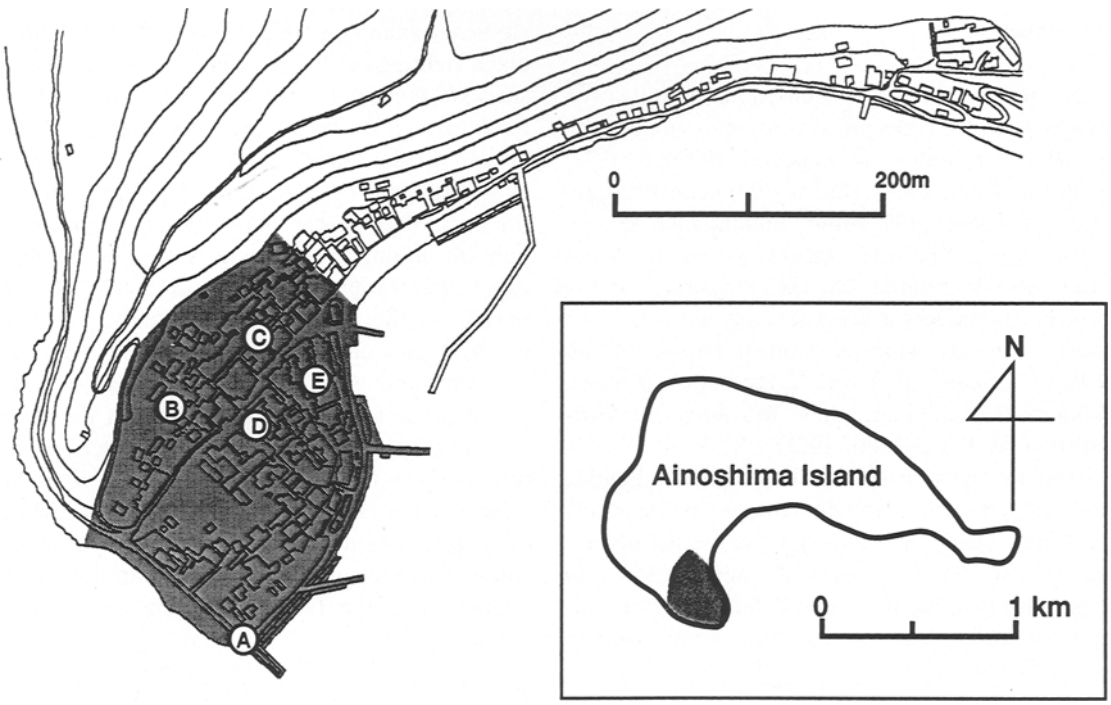

Fig. 1 Map of the study area. Ainoshima Island is 125 ha, and the main study area is situated at the southwest part (shaded area; 6.0 ha). The symbols A, B, C, D and E indicate the location of the garbage sites.

by the followig method: A basket with dried fish placed in it as bait was attached to a scale, which was then placed in the study area. The cat's body weight was obtained when the cat jumped into the basket to eat the bait. To determine the accurate date of the first estrus of female in 1993, we started daily surveys from 7 January 1993, because the first female estrus in 1989 began late in Januray (Yamane et al. 1994). Female estrus was recognized only by the presence or absence of the courting males around her. The first female estrus was documented on 20 January 1993, and 25 females came into estrus by 31 March. This period from 20 January to 31 March was then defined as the estrous season.

We observed the mating behaviors only in the daytime, because the observations at night required a torch lamp, which greatly disturbed the cats' behavior. On every morning during the estrous season, the estrous condition of all females in the study area were checked first. When an estrous female was found, the male mating behaviors toward her were observed for at least one hour a day. The male mating behaviors that we recorded were the courtship behavior, copulation, and the agonistic encounters between males. We defined "copulation" as the mount with intromission. The method used to determine whether mounts were with intromission (copulation) or not, were followed by that of Natoli & De Vito (1991): "When intromission occurred, the female emitted a sharp cry, showed an aggressive reaction by turning toward the male and threatening him, and usually rolled on the ground vigorously afterwards". Some estrous females were averse to being observed. This inevitably made the observation time of the males that courted mainly these females short. So the total observation time of courtshop behavior for each male over the estrous season varied individually from 20 to 1226 minutes. We calculated the copulation rates for each male by dividing the total observation time during an estrous season into the number of copulations observed. The copulation was scarce to observe (one copulation per 4.9 hr's observation), therefore the copulation rate calculated by too short an observation time would not be a suitable index for evaluating the mating success of the male. For these reasons, the males that had total observation time of courtship behavior less than 5 hours, were omitted from this analysis.

Each agonistic encounter between males was judged as a win or a defeat by the following method: (1) when two individuals confronted and threatened each other, the one that retreated was regarded as the loser, and the one that stood his ground was the winner, (2) when one threatened, and another one retreated, the threat-giver was regarded as the winner, and the one that retreated was the loser, (3) when one approached and another one retreated, the approaching individual was regarded as the winner, and the one that retreated was the loser.

The physical distances between an estrous female and each courting male were continuously recorded at one minute intervals (instantaneous sampling method, Lehner 1979). The measurement of this distance was estimated with the naked eye, using the female body length as a scale. The body length of the females was assigned a value of 50 cm, using data from the mean body length of females measured in 1990, which was 49.3 ± 0.6 cm ($\pm$SE, $n=11$). In evaluating the distance for each male, we first calculated the mean courtship distance for each day when they courted a female. Next, we calculated the mean courtship distance over the estrous season for each male, by dividing the number of the days that they courted a female into the sum value of the mean courtship distance of each day.

Results

(1) Distributions of Male Body Weight and Age

The mean body weight of the sexually matured males was 3.6 ± 0.1 kg ($\pm$SE, $n=46$). The distribution of body weight is shown in Fig. 2a. The mean body weight of the sexually matured females was 2.8 ± 0.1 kg ($n=19$), which was significantly smaller than the males (t-test, $T=5.9$, $p<0.001$, $df=63$). Males were grouped into three classes according to their body weight; light (2.5—3.25 kg, $n=12$), middle (3.25–4.0 kg, $n=20$) and heavy class (4.0–4.75

kg, n=14). The ages of all sexually matured males less than 5 years old were known. The distribution of the male age and compositions of body weight class for each age class are shown in Fig. 2b. More than half (58%) of the males in the study area were in the oldest age class (≥5 years old).

(2) Agonistic Encounters between Males

We observed 88 cases of agonistic encounters between males during the estrous season. We first examined the effect of male body weight on fighting success. Out of 84 agonistic encounters, 7 were those between the males of the same body weight. Of remaining the 77 encounters, 56 (72.7%) cases were won by the heavier males, and 21 (27.3%) cases by the lighter males. These values were significantly different from the expected fifty-fifty values (χ^2-test, $\chi^2=15.9$, $p<0.001$, $df=1$).

We also examined the situation where the heavier males were defeated by the lighter males. Of the 21 agonistic encounters that resulted in the winnings of the lighter males, 11 (52.3%) encounters were cases where the heavier males were away from their own group and were visitors to the groups (feeding sites) of the lighter males, 7 (33.3%) encounters were cases where both of them were away from their own groups, 3 (14.3%) encounters were cases where both fighters were visitors to the other groups. No case was observed where the lighter male was the visitor, and the heavier one was in his own group.

As for the effect of age, of the total 88 agonistic encounters, 44 were those between the males of the same age class. Of the remaining 44 encounters, 25 (56.8%) cases were won by the older males, and 19 (43.2%) cases, by the younger males. These values did not differ significantly from the expected fifty-fifty values ($\chi^2=0.8$, $p=0.31$, $df=1$).

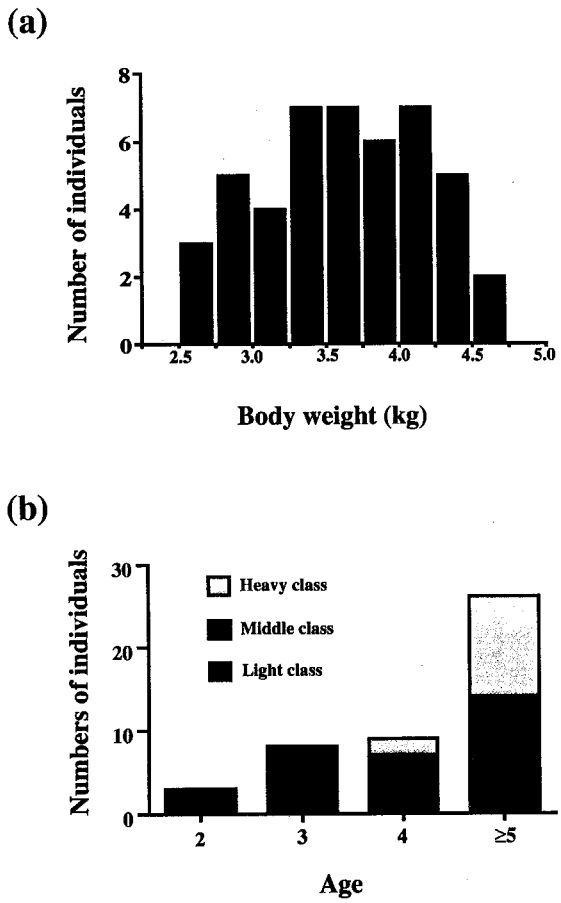

Fig. 2 Distribution of sexually matured males; (a) body weight, (b) age.

(3) Courtship Behavior and Male Rank during Courtship

In 1993, we documented the first female estrus on 20 January, and subsequently, 25 females came into estrus by 31 March (Fig. 3). Of these 25 females, 5 females came into estrus twice. The mean duration of one estrous cycle was 5.28±3.63 days (±SD, n=30). In this estrous period (from 20 January to 31 March 1993), males displayed the peculiar rutting behaviors such as frequent rubbing and urine spraying to the vertical objects (e.g., pole and wall), rutting cry, courtship, and copulation. Whenever a female came into estrus, the males aggregated and courted her. The mean number of males which simultaneously courted a female per day was 3.34±2.29 (±SD, n=102), ranging from 1 to 11. The courting males would try to approach and copulate with the estrous female. It was found that the males could approach the female only to a certain distance and no further, because they were hindered by threats from other courting males. Therefore, the distance between each courting male and an estrous female was seen as an important index in eva-

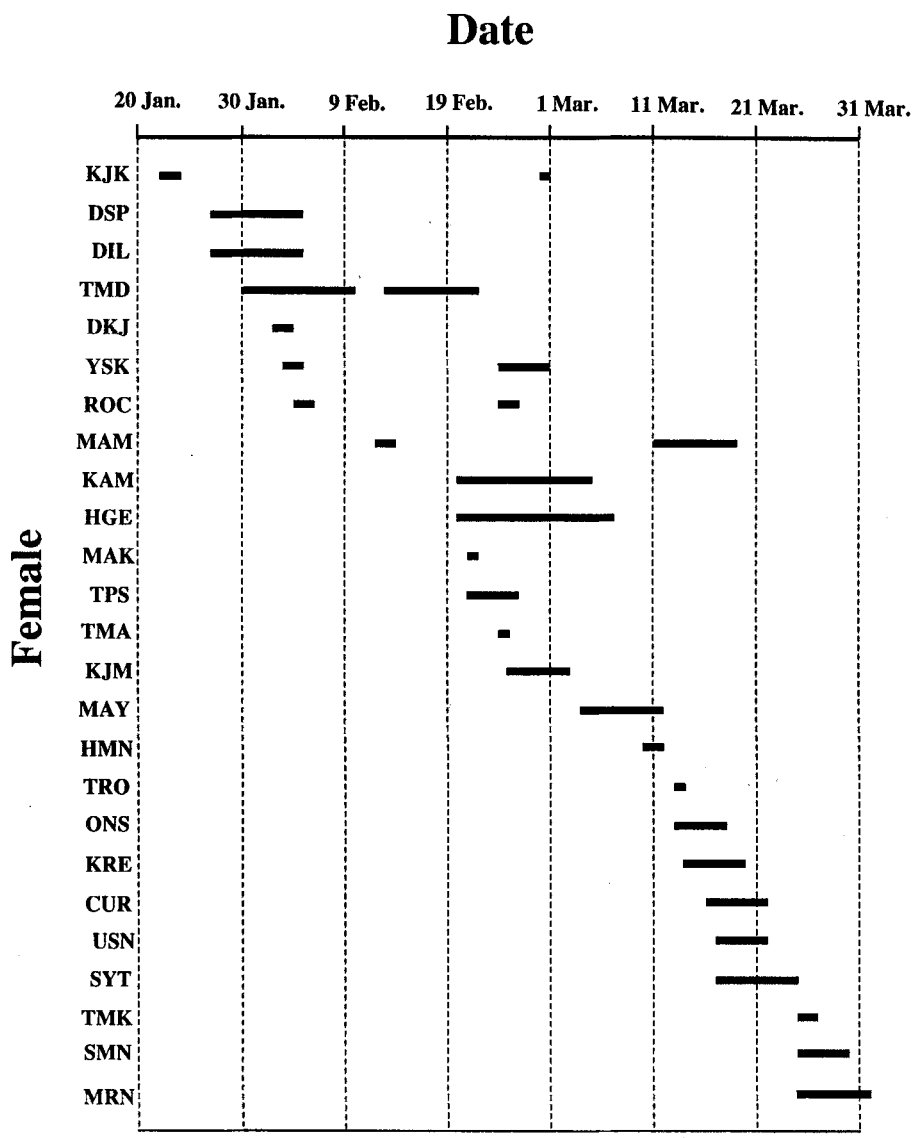

Fig. 3 Distribution of female estrus in the study area from 20 January to 31 March 1993.

luating the male rank during courtship, and will be defined as the "courtship distance" here. This courtship distance varied individually and ranged from 0 to 10 m.

Mean courtship distances over the estrous season of males in each body weight class are shown in Fig. 4a. There was significant difference among the values of each body weight class (Kruskal-Wallis test, $H=9.5$, $p<0.01$). There was also a significant negative correlation between the individual mean courtship distance over an estrous season and the body weight ($r=-0.37$, $p<0.05$, $n=40$). Mean courtship distances over the estrous season of males in each age class are shown in Fig. 4b. There was significant difference among the values of each age class ($H=11.9$, $p<0.01$).

We also examined the effect of the group that the female belonged to; whether the courted females were members of the same group as the courting males or not. Of the 48 sexually matured males in the study area, 31 (64.6%) males belonged to one of 5 feeding groups. Seventeen males out of these 31 group-

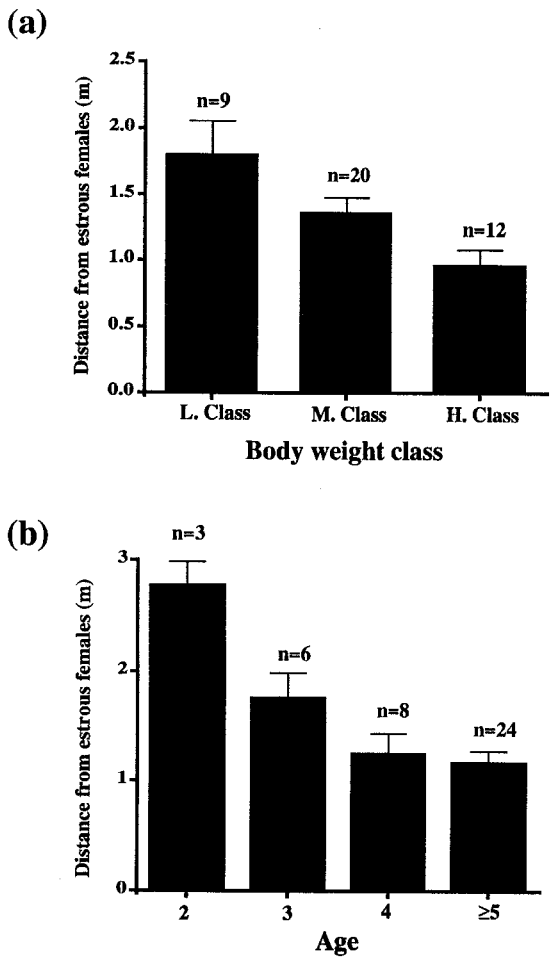

Fig. 4 The mean distance (±SE) between the courting males and the estrous females over an estrous period; (a) for body weight class, (b) for age class.

ing males, courted both females of their own group, and females of the groups other than their own. For these 17 males, we calculated the mean courtship distance in two cases: when they courted the females of their own group, and when they courted the females of the groups other than their own. The mean courtship distance when they courted the female of their own group was 0.96±0.1 m (±SE, n=17). The mean distance when they courted females of the groups other than their own was 1.54±0.27 m (n=17). The difference between the pair values was significant (Wilcoxon signed rank test, $Z=-2.88$, $p<0.005$, n=17). This result means that males could not approach estrous females of the groups other than their own as closely as they could when they courted females of their own group.

(4) Copulation

We observed a total of 46 copulations by 28 pairs from 20 January to 31 March 1993. Figure 5 shows the mean courtship distance of each courting male on the day when the copulation was observed. Copulations were conducted by the dominant males, who occupied a closer position to the females than the other males. The courtship distance on a day when copulation was observed, was 0.57±0.08 m (±SE, n=27) in the males which were observed to copulate and 1.53±0.16 m (n=65) in the males which were not observed to copulate, and the difference between them was significant (Mann-Whitney U-test, $U=227.5$, $p<0.01$, n=27, 65).

The body weight of the individual males significantly correlated with the number of observed copulations ($r=0.42$, $p<0.005$, n=46) and the copulation rates (Fig. 6a, $r=0.48$, $p<0.05$, n=20). As for the effect of male age, the mean copulation rate of the oldest age class was not so high compared with that of the 4 years old class, although the oldest class includes all males more than 4 years old (Fig. 6b). Neither the copulation rates of individual males nor the number of observed copulations significantly correlate with the age of the male, when assuming that all the males in the oldest class are 5 years old ($r=0.16$, $p=0.48$, n=21 and $r=0.28$, $p=0.054$, n=48, respectively).

Out of a total of 31 copulations by the grouping females, 24 (77.4%) were conducted by males of the same group, 4 (12.9%) were by males from outside groups, and 3 (9.7%) were by the non-grouping males. These results means that grouping females copulated more frequently with the males of the same groups.

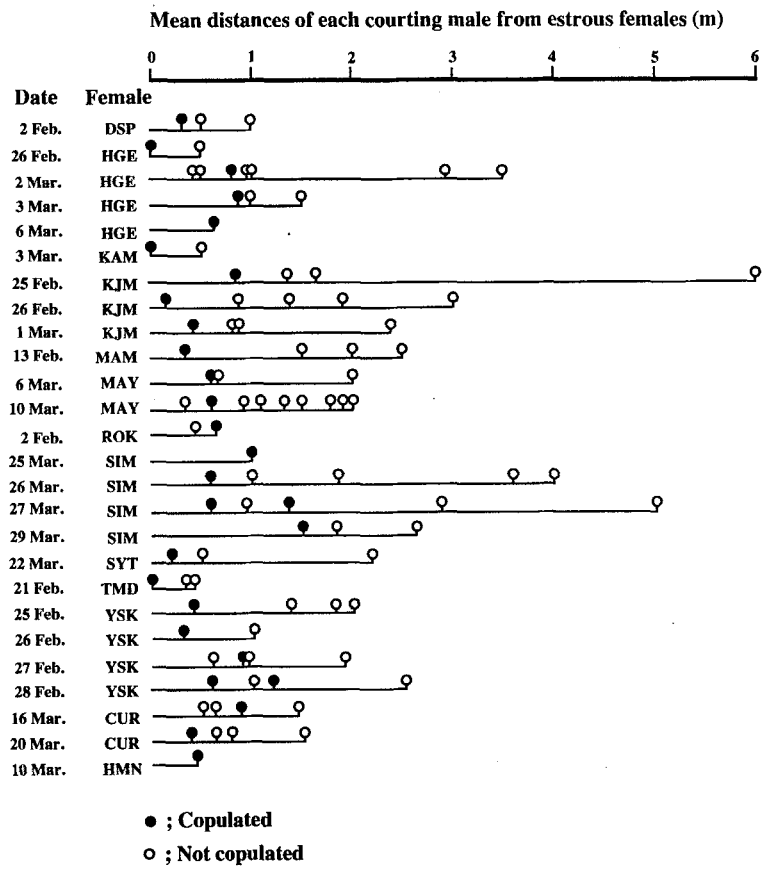

Fig. 5 The mean courtship distance between the courting males and an estrous female on a day when the copulations were observed. Solid circles indicate the males which were observed to copulate. Open circles indicate the males which were not observed to copulate.

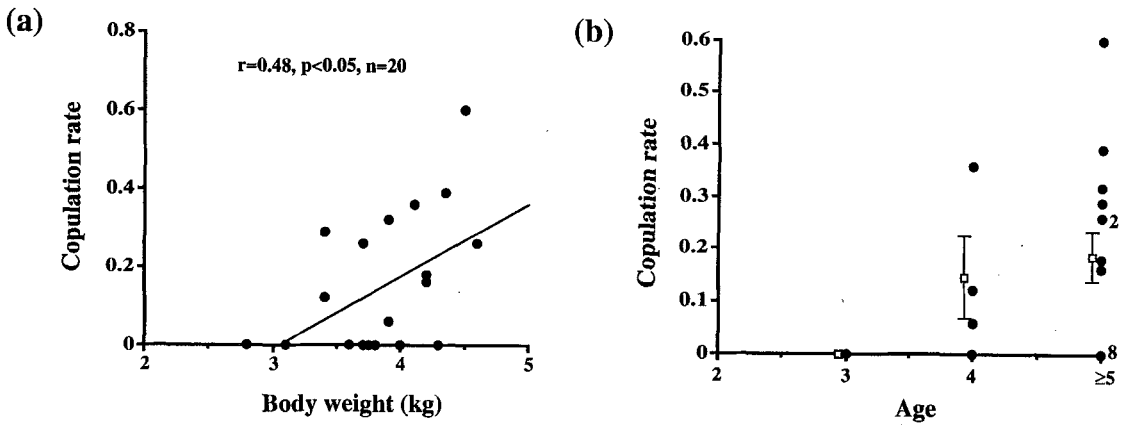

Fig. 6 Relationships between the copulation rate (no. of copulations per hour) and (a) body weight of male, and (b) age of male. The males, of which observation time were less than 5 hours, were omitted from this analysis. The figure right side of solid circles means the count of the same point. Squares indicate the mean values (±SE) of each age class.

Discussion

In polygynous mammalian species, males compete intensely with their rivals for mates. This competition usually results in larger males frequently getting higher social rank and then having higher mating success than smaller males (e.g., red deer: Clutton-Brock et al. 1982; elephant seal: Cox & Le Boeuf 1977).

The feral cats in this study showed sexual dimorphism in their body weight, and their mating system is "scramble competition polygyny" (Davies 1991), therefore the severe male-male competition for mates was predicted, especially in this study's high density and group-living population. Male cats became aggressive during the estrous season, and agonistic encounters between males were frequently observed during courtship. The results from the agonistic encounters between the males indicated that heavier males frequently won over the lighter males. The same tendencies are reported in several studies of polygynous mammalian species (red deer: Clutton-Brock et al. 1982; African elephant: Poole 1989). Therefore, it is suggested that the body weight is one of the important factors influencing the fighting ability of the male cats.

During the estrous season, male cats roamed a larger area than usual (Yamane et al. 1994; Liberg & Sandell 1988; Izawa 1984), and the female in estrus was usually courted by several males simultaneously. Courting males attempted to approach an estrous female while threatening other males. Some males were able to come within close proximity to a female, while other males were unable to approach at all because of interference from competitors. From the results of this study, the courtship distance could be regarded as a good index of male rank during courtship. The mean courtship distance during the estrous season significantly correlated with body weight, and this suggests that body weight affects courtship rank. Estrous females were found to copulate with the males having high courtship rank. Thus, it is deduced that the heavier males have a greater chance to copulate than the lighter males. In fact, copulation rates significantly correlated with the body weight of males. It is clear that body weight was one of the most important factors that influenced fighting ability, courtship rank, and the mating success of male cats. In this population of feral cats, the heavier males have higher courtship rank and therefore enjoy greater mating success, as was shown in several studies on the polygynous mammalian species.

There are several studies in mammalian species about the relationships between age and social rank, and mating success. In red deer, both fighting success and reproductive success increased with age, peaking at 7 to 10 years old, then declined rapidly after the age of 11 (Clutton-Brock et al, 1979, 1988). Poole (1989) showed that the mating success of male African elephants increased with age up to 50 years old.

In this study, the age of males more than 4 years old were unknown, and so the age distribution of the males was largely biased to the oldest age class ($\geq$5 years old). For this reason, it was difficult to evaluate with accuracy the effect of age on courtship rank and mating success. In agonistic encounters between the males of different age classes, the older males did not often win over the younger males. Moreover, the mean courtship rank and the mean copulation rate of males in the oldest class was not so high. Liberg (1983) showed in his study that the oldest male (ranging from 3 to 5 years in age) in the feral cat population could approach much closer to the estrous female and monopolize the copulations. Why was there no direct effect of age on the fighting ability and the copulation rate in this study? In this study, more than half (58%) of the male cats wer older than 4 years. Thus, the oldest age class ($\geq$5 years old) included a range of males from 5 years old to a considerably advanced age. It is possible that the older males in this age class had lowered fighting ability and copulation rate of this class as had been demonstrated with the red deer whose fighting and reproductive success declined after the age of 11 (Clutton-Brock et al., 1979, 1988). We found that the copulation rates of 8 males in the oldest age class, were zero (Fig. 6b). Their body weight (3.6 ± 0.23 kg, $\pm$SE, $n=7$) was lighter than that of the other males in the same age class (4.1 ± 0.15 kg, $n=8$), although there was no significant difference between them (t-test, $T=2.1$, $p=0.06$,

df=13). It is clear at least, that these lighter males lowered the copulation rate of this class. It is unknown, however, whether the lighter males were considerably old or not. In any case, male age in this feral cat population did not affect the male mating success as directly as male body weight.

Males expanded their home range during the estrous season (Yamane et al. 1994) and some males visited and courted the females of groups other than their own. Similar results were reported by Izawa (1984) and Liberg (1981). When the grouping males courted the females of feeding groups other than their own, they were sometimes defeated by the lighter males, and their courtship rank dropped. These results show that courtship rank is changeable according to the male's location, and the categories of females they courted (same group member or not). This also suggests that the male courtship rank is influenced not only by physical factors like body weight, but also by the local factor (whether they are inside or outside their feeding group). Izawa (1984) showed that 84.0% of the pairs of "mating" (including all behaviors of courtship and mating) were observed within the same groups. The present study also showed that the majority of observed copulations were conducted by pairs within the same groups, and that inter-group copulations were rare. One of the reasons why the majority of the copulations with the grouping females were conducted by the males of the same group, will be that outcoming males had fewer opportunities to copulate because of their lowered courtship rank.

To date, there are only a few studies investigating the mating strategy of the male feral cats (ex. Natoli & De Vito 1988, 1991, Liberg 1983). More studies in various types of cat populations will be necessary to clarify the mating system of the feral cat, and to provide clues to the mating systems of the other wild felids that are difficult to observe. The effect of male location on courtship rank and mating success will be important in discussing the male reproductive strategies of the group living feral cat.

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