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ヤマネコ類の社会維持機構の解明ー特にテリトリー獲得過程における雌雄差による分析ー

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FLEXIBILITY OF THE SOCIAL SYSTEM OF THE FERAL CAT, *FELIS CATUS*

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SUMMARY

Most species of felid have an exclusively, solitary social system, adopt a territory-based spacing pattern, and occur at low population densities. This has been attributed to their stealth and ambush hunting strategy, where group interactions are not, in most cases, required for hunting success. One exception to this general rule is the feral cat *Felis catus*, where large inter-population differences in density and social system are known. This species thus affords an unique opportunity to study the effects of population size and resource availability on the social system of a felid.

We made detailed ecological comparisons among several populations of feral cat living under conditions of different resource availability, primarily food and shelter. We were able to show that those cats living in populations where resources (mainly food and shelter) were predictable, clumped and abundant, formed groups and achieved high population densities. Conversely, those in areas of unpredictable, dispersed and scarce resources occurred at low population densities and adopted a solitary life style, generally reverting to the ancestral hunting strategy. Social and demographic characteristics of populations showing features intermediate between these extremes in population density and in social system were correlated with the predictability and amount of resource availability at their population.

The documented differences in social system were also reflected in the genetic constitution of the population. In the social system which evolved under conditions which permit high population densities, younger individuals need not disperse to establish their own hunting territories. Extensive intra-group mating occurred, and groups thus consisted exclusively of relatives, especially related females, which showed a stronger natal philopatry than males. Under the solitary social system, a male mated with any receptive female he encountered in his territory, which was often located far from his natal site.

Accordingly, the degree of relatedness of members of such populations was much lower than that seen in high density populations. We conclude that detailed studies of the social system of feral cat populations under conditions of different resource availability, performed in tandem with genetic analyses, present an ideal opportunity to investigate the role of ecological effects in shaping a species' social system, and will reveal much of the evolution and diversity of the social systems seen in wild felids.

INTRODUCTION

Recent studies on felids have revealed the solitary social system seen in most members, including *Felis libyca*, the ancestor of the domestic cat, to be due to their having evolved and maintained a hunting strategy of stealth and ambush. The only three known exceptions to this trend are the mother-young group and male peer group of the cheetah *Acinonyx jubatus* (Eaton 1969, 1970), the pride and coalition of the lion *Panthera leo* (Schaller 1972, Bertram 1973, 1975a,b, 1976, Bygott & Hanby 1974, Bygott *et al.* 1979, Rundai 1979), and the stable groups of the feral cat *Felis catus* existing under conditions of high population density (Izawa *et al.* 1982, Natoli 1985). Why, among the felids, do only these three species show a group formation, and how has this phenomenon been acquired in the evolutionary course of felid social systems?

The domestic cat, *F. catus*, was first domesticated in ancient Egypt from a group of small felids closely related to *F. libyca* (Todd 1978, Corbett 1979). The domestication of the cat has had an entirely different purpose from that of other domesticated animals, such as cattle, horses, sheep, pigs and dogs. The latter have been domesticated for farm production of meat, milk, skin products or wool, or for use as labour animals, be it agricultural work, transportation, hunting, etc. One consequence of this has been that the reproduction and movement of these species has been controlled. In contrast, the original purpose of domestication of the cat was rodent pest control. In return for protection of grain stores from rodents, cats were provided with some form of shelter and food and, unlike other domesticated animals, no control was placed on their reproduction or movement. Accordingly, the cat has become widespread in many countries along with the spread of human beings. Together with the ability of the species to adapt to a feral lifestyle, these features have meant that feral cats are now encountered in a wide variety of environments throughout the world.

We have studied the ecology of the feral cat, especially in relation to the intraspecific variation seen in the social system. Our findings strongly suggest that an understanding of the flexibility of social systems seen in the feral cat will provide an insight into the origin and diversity of the social system of felids in general.

Population density of feral cats

Population densities of feral cats reported in the literature range from $1/\text{km}^2$ (Jones & Coman 1982) to over $2000/\text{km}^2$ (Izawa *et al.* 1982, 1990, Natoli 1985). This variation is believed related to differences in ambient food availability (Liberg & Sandell 1988).

Like wild species of felids, feral cats living in the forest and grassland and separated from human contact are hunters, hunting small animals, and occurring at

low population densities (Apps 1983, Liberg 1980, 1981, 1983, 1984, Jones & Coman 1982, Langeveld & Nievold 1985, Fitzgerald & Karl 1986).

Feral cats living in urban areas are heavily dependent upon human beings for survival, either directly, by obtaining food provided by cat lovers, or indirectly, by obtaining food by scavenging among refuse. The abundance, quality and availability of refuse varies greatly in relation to the density and life-style of the human population present. One of the best of such conditions for the feral cat is found in Ainoshima Island, Japan. Here, feral cats inhabit a fishing village, where large volumes of waste material from fish processing are dumped at several local refuse sites around the village. The extremely high population density recorded, 2350 cats/km², persisted throughout the 6 year study period (Izawa *et al.* 1982, Izawa 1984). In comparison, the feral cat population in Shingu, located on the mainland opposite Ainoshima Island, is also dependent on refuse (Izawa 1984), but here refuse is collected regularly and disposed of by local government, restricting the temporal access of feral cats. As a result of this lower availability of food viz refuse, the feral cat population at Shingu is at a much lower density than the population at Ainoshima Island.

Feeding by cat lovers can also play an important role in increasing the population density. Feral cats living in Junin-machi, Nagasaki, Japan, in Rome, Italy, and in Portsmouth, U.K., all gained the major portion of their food through provisioning by cat lovers, such that when sufficient and high quality food was given regularly, the population density increased to levels higher than that seen in the fishery village of Ainoshima (Table 1).

Several favourable environmental factors were responsible for the highest population densities recorded in Junin-machi (Izawa *et al.* 1990). First, the food available to feral cats was both abundant and of high quality, consisting of both fish remains scavenged from refuse tips and of high quality items provided daily by cat lovers. Second, many traditional wooden houses remain in this area. These provide the cats with many resting and breeding sites, unlike more-modern housing. Third, the steep and narrow paths, often stepped, severely restrict vehicle access, and road kills are therefore few. Also the mild climate results in a low winter mortality of kittens. The latter two conditions mean that both adult and juvenile mortality at Junin-machi is much lower than that seen in populations in other areas.

A clear relationship was evident between the population density of feral cats and ambient food conditions. The several other factors which may also affect the density of the feral cat population, e.g. presence of resting and breeding sites, traffic conditions, presence of free-ranging dogs, etc., play only a minor role in relation to that played by food conditions.

Social system of Felids

Social system of wild felids

It is generally considered that wild felids hunt prey animals by stealth and that, except for the lion and cheetah, they are thus adapted for solitary living within a more-or-less exclusive home range or territory (Eaton 1976, Kleiman & Eisenberg 1973). However, data for many species are inadequate, and it is not yet possible to perform a meaningful comparison. Several species are well known, however. Corbett (1979) reported that the Scottish wildcat *F. silvestris*, lives a solitary life, and that females maintain home ranges discrete from those of other females. Similar patterns have been described for the lynx, *Lynx lynx* (Haglund 1966) and the bobcat *L. rufus* (Bailey 1972, 1974), both of which show inter-male and inter-female territoriality. The tiger, *Panthera tigris*, also shows a typical solitary social system and inter-sexual territorial spacing pattern (Schaller 1967, Eisenberg & Lockhart 1972, Sunquist 1981, Panwar 1987), as does the leopard *P. pardus* (Muckenhirn & Eisenberg 1973).

Our ongoing studies have yielded some information on the spacing patterns of the two species of small Japanese wild felids, the Iriomote cat, *F. iriomotensis*, and the Tushima leopard cat, *F. bengalensis euphilura*. Both species hunt small animals; lizards, birds and rodents for the Iriomote cat, and mainly wood mice for the Tushima leopard cat. The Iriomote cat lives within a home range of average area 2.96km² for males and 1.75km² for females. Each female maintains a fairly stable home range, the borders of which are generally discrete or contiguous with those of female neighbours (Figure 1). In contrast, the home range of a male shows extensive overlap with the home ranges of neighbouring males, and with those of females (Figure 2). Preliminary analysis of our data on the Tushima leopard cat indicates the species to be solitary. Males occupy home ranges of ca. 0.95km² which overlap extensively with those of neighbouring males and females. Data are insufficient to comment on the distribution pattern and size of the home ranges of females. Therefore, both these species are solitary, and show territoriality as part of their spacing system.

Feeding group of feral cats In Ainoshima Islan

The social organization of the feral cat was first investigated by Leyhausen (1956, 1979), who believed the species to be exclusively solitary, reporting that both males and females occupied discrete territories like wild felids. Females tended to defend their territories more fiercely than did males. Even where territories overlapped, territory owners did not always show mutual tolerance, instead actively avoiding direct encounters through the use of visual and olfactory stimuli. He later discussed the variation of the social system of the feral cat, including group formation, reported from studies throughout the world (Leyhausen 1988).

However, group living or feeding groups have subsequently been documented in feral cat population. One such example is provided by our studies on Ainoshima Island (Izawa *et al.* 1982), where the feral cat population depends mainly on refuse as a food source. The five refuse tips (feeding sites) with their stable year-round supply of food may play an important role in the survival and social organization of the cat

populations on this island. The individual membership of groups using each respective feeding site remained almost constant, and the members of each group are therefore considered here as constituting a 'feeding group'. Individuals within a feeding group had overlapping home ranges, utilized common resting sites, and showed no aggressive behaviours towards one another. The feeding group is thus not simply an aggregation of individuals utilizing the same feeding site, but rather is a more organized group in which social interrelationships develop. The group sizes (number of cats in a group) varied from 10 to 44, depending on the abundance of food resources at a feeding site.

The primary unit of the social system of the feral cat on Ainoshima Island is the mother-offspring bond (Izawa & Ono 1986). Females deliver their kittens at established breeding sites. Although infant mortality was high, those individuals which achieved adulthood established their own home ranges, which overlapped extensively with that of their natal area. Furthermore, these individuals are permitted to use the same feeding site as their mother, and to join the membership of the mother's feeding group. This continual process of kin recruitment seems responsible for the formation and maintenance of the feeding group structure. Male offspring, however, showed less adhesiveness to their natal area than females, and were apt to disperse beyond the feeding group by the time they attained full adulthood.

Although the mating system within each group is promiscuous, genetic analysis and observations of mating behaviour of several feeding groups clearly demonstrated their genetic independency, indicating a large proportion of mating to occur within the group.

Spacing pattern of the feral cats in Shingu

In addition to the refuse food resource described earlier, the feral cats in Shingu also utilized a less abundant and patchily distributed food resource (Figure 3). All individuals were classified into one of two types; resident or non-resident. On average, females had smaller (0.42km^2), more stable home ranges than did males (0.79km^2). Roaming of non-resident adult males was also a conspicuous feature at this site. The cats were also categorized according to their behaviour pattern, into aggregating and solitary. The aggregating cats used overlapping ranges, and shared common feeding and resting sites. This behaviour closely resembled that of the feeding group seen on Ainoshima Island, and the spacing pattern of the feral cat at Shingu was evaluated as a miniature of the solitary and the group.

Spacing pattern of the feral cats in Junin-machi

As noted earlier, the highest density of feral cats known to date is that of the population at Junin-machi, Nagasaki, at 3100 cats/km^2 (cf. Liberg & Sandell 1988).

Group membership at each of the five feeding sites at Junin-machi was constant (Izawa *et al.* 1990). Sites E and S were provisioned by cat lovers, sites T and Z were refuse tips, and site H was both a refuse tip and a hand-out place. The group sizes and home ranges of these five feeding groups are shown in Figure 4. These groups superficially resemble the feeding groups seen on Ainosshima Island, but differed markedly in the utilization pattern of resting sites by group members (Figure 5). Usually, feral cats living in an urban area had one to three resting sites, such as in vacant or derelict buildings, beneath floors, etc. In Junin-machi, however, two distinct types of utilization pattern were observed; one where members utilized many resting sites scattered throughout the home range, as seen in the feeding group on Ainosshima Island, and another where members were concentrated together within a small resting site, e.g. in a small box.

This is the first documented example of common use of resting sites by feral cats. One factor facilitating this phenomenon may be the stronger relatedness of component group members. In some groups, under the ambient conditions of a stable and abundant food supply, the dispersal of kittens occurred at low frequency, and offspring and adults formed a closely related kin group which shared resting sites. Thus, in the presence of an abundant and clumped food resource, feral cats can drastically modify their social system from one where a feeding site is monopolized by several non-related individuals, to one of a feeding group composed of related individuals. Additionally, the loss of inter-individual territoriality within the kin-group effects a further step in the variation of flexibility in the social system. The utilization of common resting sites enables the cat population density within a given area to far exceed that possible under a simple feeding group system.

The determinant factor of group size of the feeding group

In the lion, pride size is determined by the number of females which have kinship interrelationships, with reproduction and survival of cubs being affected by social factors. It has also been reported that pride size may also be greatly influenced by food availability, prey size and hunting efficiency (Caraco & Wolf 1975, Bertram 1973, 1975b, Lamprecht 1978, Macdonald 1983). The group size of the feral cat was also correlated with relative food abundance. However, the quantitative estimation of food abundance poses numerous problems. To analyze the effects of food resources on the Ainosshima population we therefore devised an index of potential food availability. We assumed the amount of refuse produced by one family of human residents to be constant among families, and regarded the number of families using a particular refuse bin or dump as an index of relative food abundance. The resultant relationship between food abundance and group size is given in Figure 6. Group size increases linearly with food abundance up to a group size of five individuals. Were group size limited solely by food abundance, this linear trend would be expected to continue, as illustrated by the broken line. However, for each of groups C, I and Z,

group size is less than the expected value. One explanation is that group size may subsequently increase to attain the expected value. However, group size was relatively constant throughout the study period, suggesting the respective habitat of each group to be at maximum carrying capacity, at a value lower than that predicted. As such, food abundance is not the sole factor influencing group size, and it is likely that factors such as resource availability, e.g. resting and breeding sites, social relationships among individuals, and the number of individuals that can come to a feeding site at one time, are also important factors.

Variation in the social system of cats

Among the felids, intraspecific variation in social system has also been reported in wild species and is not restricted to the feral cat. For example, habitat-related differences in spacing pattern were observed in the bobcat in the USA; in Idaho and Alabama, home ranges of both males and females show only slight overlap, in Minnesota males have overlapping ranges, while in California and Tennessee both sexes have overlapping home ranges (Bailey 1974, Berg 1979, Miller & Speake 1979, Zezulak & Schwab 1979, Kitchings & Story 1984).

The lion also shows variation in its social system (Leyhausen 1988). Lions in the African savanna typically live in a well-organized social group, the pride. In the desert areas of northern and south-western Africa, however, they form only pair or pair-offspring groups, while in the semi-desert areas of south-western Africa, groups consist of a single male and several females. Seasonal differences are also evident; in the Kalahari, prides are formed during the rainy season, but revert to pairs or pair-offspring groups at other times of the year. Harsh environmental conditions, with few prey animals and a severely restricted water supply, seem to result in a decrease in the group size of lions.

Liberg and Sandell (1988) summarized the information on the densities of feral cat populations in various environments throughout the world. The feral cats in the above three environments lived at higher density than those in other areas in Table 1.

The fundamental social system of felids is solitary, and this social system is most adaptive for their hunting style of stealth and ambush. Our studies of the Iriomote cat and the Tushima leopard cat revealed them to show basically similar spacing patterns to that seen in the solitary-living feral cat, suggesting feral cats living by hunting to have solitary and exclusive home ranges, as seen in the wild felids. With such a social system, however, feral cats are unable to attain a high population density, even under extremely favourable food conditions, as the feral cat in semi-arid areas of Australia (Izawa *et al.* unpublished). As the minimum territory size determines the maximum capacity, the population density of the cats could not increase beyond a certain level.

Under conditions of increasing food availability, feral cats can increase their fitness by changing their spacing pattern. By abandoning their instinctive

exclusiveness to relatives, but not to other individuals, they can form an exclusive kin-related group and occupy a group territory. The size of the group varies according to the abundance of the food resource. Feral cats living at high densities in other parts of the world showed a similar group organization to that seen on Ainoshima Island (Laundre 1977, Macdonald & Apps 1978, Dards 1978, 1983, Corbett 1979, Liberg 1980, 1981, Panaman 1981, Izawa 1984, Natoli 1985).

Laundre (1977) made a comparative study of farm cats under solitary and group life styles. He found some small social groups, these being formed solely to use the milk supplied by farm workers. However, the vast majority of the cats adopted a solitary life style, which, in this environment, is more advantageous because the cats have to obtain their food mainly by hunting.

Dards (1983) studied feral cats at dockyards, especially the relationship between the female group and males. Some mature male dockyard cats ranged over the areas of several groups of females and their offspring, whereas other males had only small home ranges containing one female group. The relationship among males was aggressive.

Cats inhabiting urban areas and depending upon humans to provide food can achieve higher population densities, and can also form groups. These groups have the following common characteristics; first, they are dependent on human actions for their supply of food, this being either refuse or handouts. Second, food within the habitat is abundant and clumped in distribution. Third, a distinct kin-relationship exists among females within a group. We estimate the process of the development of a social system in feral cats to proceed as follows; feral cats in rural areas that obtain their food by hunting also adopt a solitary life. In such a habitat, the food within the home range of an individual is insufficient to sustain that individual only, necessitating a solitary social system. However, with abundant food resources within the range of one individual, the young cats need not disperse to establish their own territory, and a new system develops which is not found in wild felids, group formation. The component individuals within each group consist of only relatives, especially related females, because females generally show a stronger natal philopatry than do males. The size of the group is partly determined by the amount of localized food resource. Close kinship could also allow the next step in the social system, the utilization of common resting sites, which will further contribute to increased population density within a given group home range.

Studies on feral cat populations throughout the world have described a similar social system. It is essential that the degree of relatedness of individuals within a group be examined. Schar (1983) reported that the different social systems he documented among various small populations stemmed from genetic differences among them. We compared the gene frequencies of the pelage pattern of two populations of the feral cat, on Ainoshima and in Shingu, but found no significant differences in gene frequencies between them. We concluded that the variation in social system observed between these two populations was not genetically determined.

However, further genetic information is required in relation to analysing the social system of the feral cat, notably to elucidate the role of maternity and/or paternity in its structure and maintenance.

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Fig.1 Spacing pattern of five Iriomote cats in October, 1983 (Izawa *et al.*, unpublished). Solid lines show the home ranges of males and dotted lines show those of females.

Fig.2 Spacing pattern of four Iriomote cats in February, 1984 (Izawa *et al.*, unpublished). Solid lines show the home ranges of males and dotted lines show those of females.

Fig.3 Spacing patterns of the feral cats in Shingu area (from Izawa 1984). Arrows show the movements of non-resident cats. a)1981, b)1982.

Fig.4 The home ranges of five feeding groups in Junin-machi (from Izawa *et al.* 1991). Closed circles denote the feeding sites. Figures in parentheses show the group size.

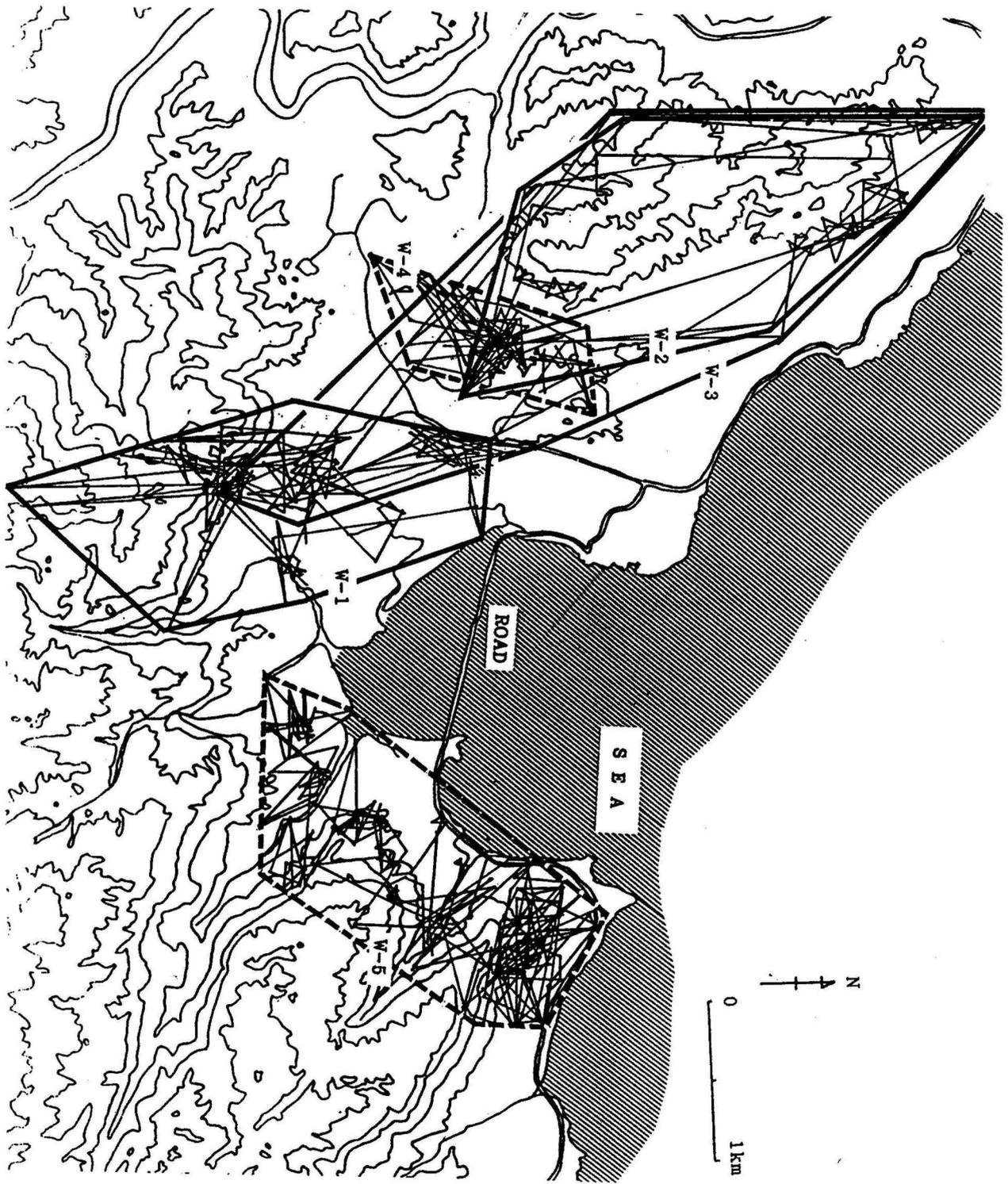
Fig.5 Distribution of the resting sites of five feeding groups in Junin-machi (from Izawa *et al.* 1991). Small letters show the locations of the resting sites of each group members.

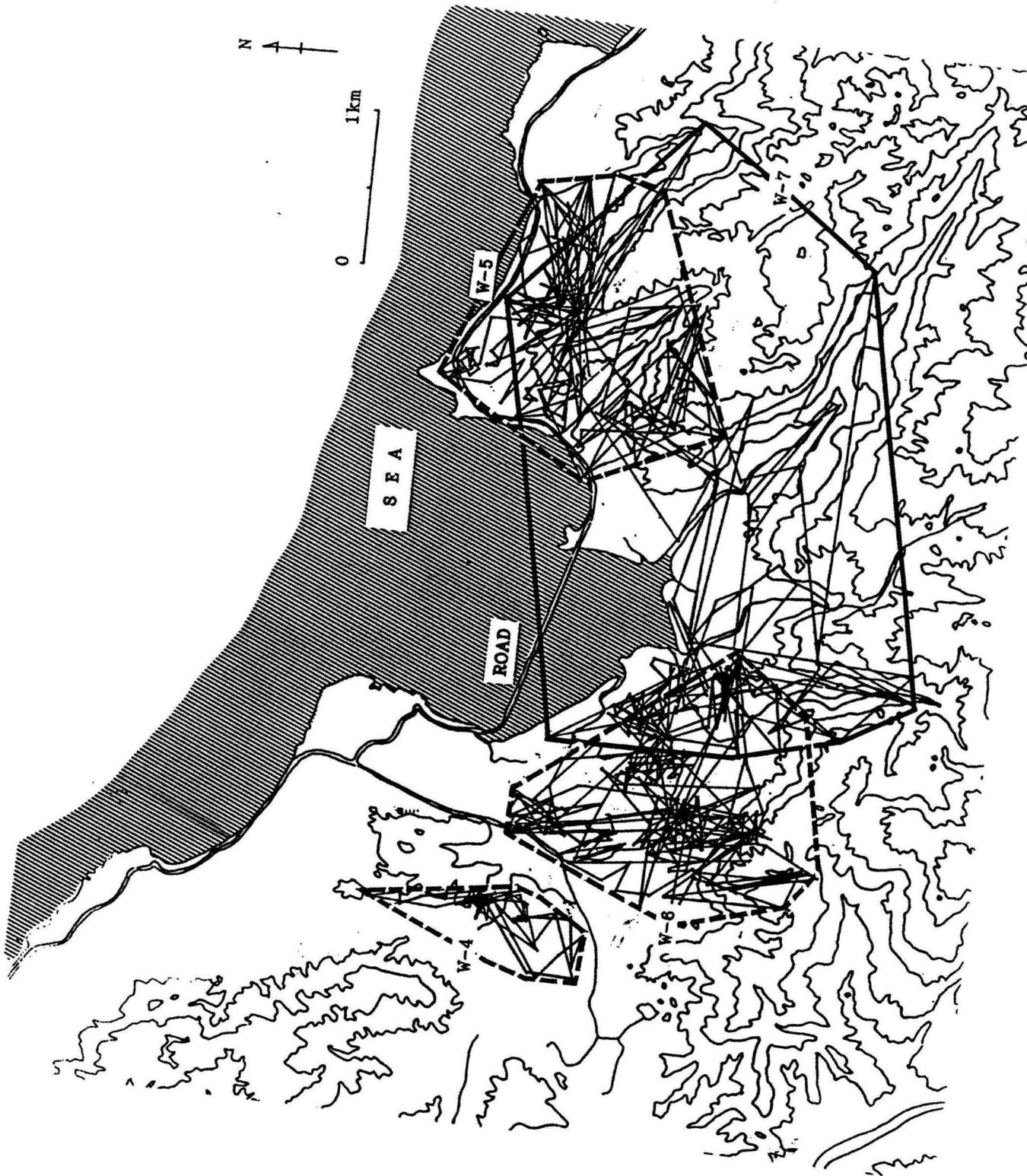
Fig.6 The relationship between food abundance and group size in Ainoshima Island.

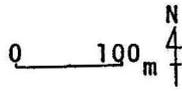
Table 1 Densities and characteristics of their habitats of the feral cat' populations
(modified from Liberg & Sandell (1988))

FOOD TYPE; G:garbage, F:feed from human, M:mild, P:small mammals, birds and other
small animals, FORAGING TYPE; S:scavenging, F:fed by cat-lovers, H:hunting
FOOD ABUNDANCE; R:rich, M:medium, P:poor, FOOD DISTRIBUTION; C:clumped, M:medium,
D:dispersed

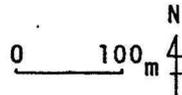
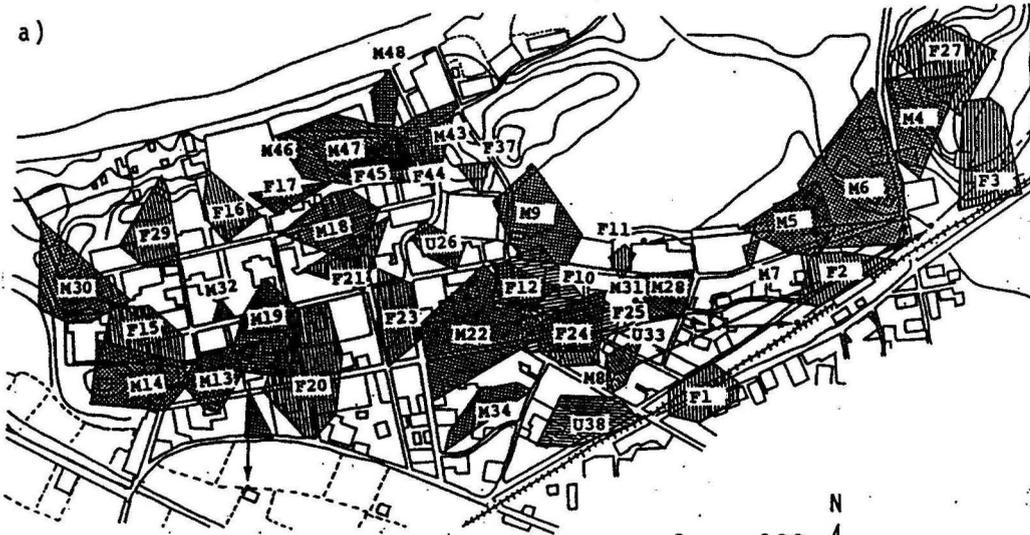
STUDY AREA	ENVIRONMENT	FOOD TYPE	FORAGING TYPE	FOOD ABUNDANCE	FOOD DISTRIBUTION	DENSITY (/km ²)	REF.
Junin-machi Japan	Urban area	G,F	S,F	R	C	3100	Izawa <i>et al.</i> (1991)
Ainoshima Japan	Fisher village	G	S	R	C	2350	Izawa <i>et al.</i> (1982)
Rome Italy	Park	F	F	R	M.C	1200 -2000	Natoli (1985)
Portsmouth U.K.	Dockyard	F	F	R	M.C	200	Dards (1978,1983)
Shingu Japan	Urban area	G	S	M	D	130	Izawa (1984)
Dassen Is. S.Africa	Subtropical scrub	P	H	M	D	20-50	Apps (1983)
Cornwall U.K.	Dairy farm	M,P	F,H	M	C,D	30	Panaman (1981)
Illinois, U.S.A.	Agricul. land	F,P	F,H	M	C,D	6.3	Warner (1985)
Yathong Australia	Semi-arid area	P	H	M	D	5-6	Izawa <i>et al.</i> (unpublished)
Macquarie Is. N.Z.	Sub- antarctic heath	P	H	M	D	2-5	Jones (1977)
Victoria Australia	Subtropical grassland	P	H	M	D	0.7-2.4	Jones & Coman (1982)
Orongorongo N.Z.	River valley Grass slopes wood	P	H	P	D	1	Fitzgerald & Karl (1986)



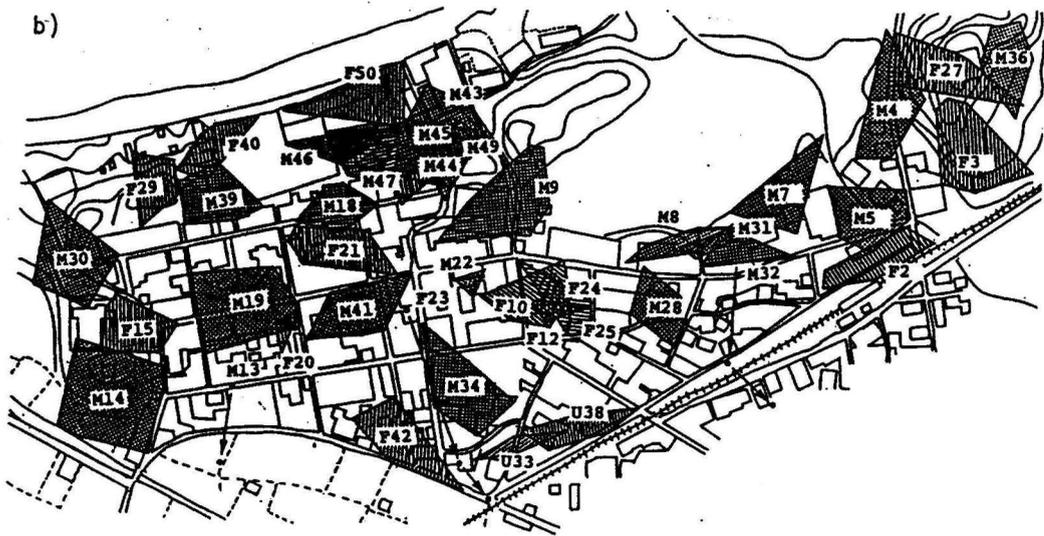




a)



b)



 male
  female
  unknown sex

