

The reproductive tactics and activity patterns of solitary carnivores: the Iriomote cat

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Abstract Felids are generally considered to be crepuscular and nocturnal in their activity, but few studies have attempted to analyze the variability of their activity patterns. We studied the daily activity of the Iriomote cat *Prionailurus iriomotensis* by radio-tracking on Iriomote Island, Japan. The general activity patterns of Iriomote cats showed slightly prevailing activity during dark periods of the day with particular peaks at dawn and dusk or during the early hours of the night. However, these patterns were clearly dependent on the sex and reproductive status of the cat. Peaks of cats' activity coincided with those of their main prey. On average, the cats were active for thirteen hours per day. During the mating season, the rhythm of activity in males followed that of breeding females, but not that of non-breeding ones. Males exhibited 11% higher

total daily activity and longer active bouts during the mating period than in the remainder of the year. Breeding females had additional mid-day activity peak during the nursing period, but their total time of activity per day was 16% lower than in the period of kittens' independence. Their active bouts were shorter and more frequent during nursing than at other times. These results suggest that lactating females perform frequent movements to and from the den site to care for kittens. During the non-nursing period, females increased their activity, possibly in response to lowered prey abundance and the need of intensive foraging to recover after lactation. Seasonal and sexual variation of activity patterns in the Iriomote cats confirmed the existence of different reproductive strategies of males and females of these solitary carnivores.

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Introduction

Variation in mammal activity patterns is dependent on a range of environmental circumstances such as photoperiod (Kavanau and Ramos 1975; Beltran and Delibes 1994), temperature (Gębczyński 2006), predator–prey interactions (Cloudsley-Thompson 1961), and competition avoidance (Hayward and Hayward 2007), but they can also be affected by behavioral processes related to reproduction (Schmidt 1999; Zalewski 2001). Felids are generally considered to be crepuscular and nocturnal in their activity (Kitchener 1991), however, they are adapted to function in a wide range of light conditions (Sunquist and Sunquist 2002). On the other hand, detailed knowledge of activity patterns of many felid species and the factors shaping them is rather limited.

The Iriomote cat, *Prionailurus iriomotensis*, is a small (3–4 kg) felid endemic to Iriomote island, Ryukyu Archipelago, Japan. Whether it is a full species or a subspecies of the leopard cat, *Prionailurus bengalensis*, has long been debated, but recently it was proposed that it be considered as a species with uncertain taxonomic position (*incertae sedis*) (Wilson and Reeder 2005). Its ecology has been studied since the early 1980s (e.g. Yasuma 1981; Izawa et al. 1991; Sakaguchi 1994; Okamura et al. 2000; Nakanishi et al. 2005), however, no data on its daily activity patterns have yet been reported.

The Iriomote cat forages on diverse prey, however, it mainly takes key vertebrates available on the Iriomote Island, such as amphibians, reptiles, and semi-aquatic birds, but also takes insects on occasion (Sakaguchi and Ono 1994; Watanabe 2003). The amphibians on Iriomote Island show generally crepuscular and nocturnal activity, whereas some bird species dominating the cat diet (such as *Rallina eurizonoides*, *Amauornis phoenicurus*, or *Turdus pallidus*) tend to be more active during the morning and late afternoon (Watanabe and Kobayashi 2006). According to the commonly accepted assumption that predators synchronize their activity with that of their main prey (Curio 1976) the Iriomote cats should show peaks in their activity in the twilight or at night, while foraging. Such a pattern was shown for the leopard cat *Prionailurus bengalensis* in Thailand (Rabinowitz 1990; Grassman 2000; Austin et al. 2007) the closest relative of the Iriomote cat (Johnson et al. 1999).

A study on the Iriomote cats' movement patterns (Schmidt et al. 2003) showed that it was highly variable as it changed between seasons and was dependent on the sex and reproductive status of the cats. These results suggested

that distances moved, speed of travel, and range of daily movements are shaped by reproductive strategies that are different in males and females. Males increased their mobility by covering larger daily ranges and moving faster during the mating period, thus indicating that movement was influenced by the need to contact females. Females, in contrast, adjusted their behavior to the need to tend to kittens and to the abundance of food. Similar causal relationships were suggested by Sakaguchi (1994) for seasonal variation in the Iriomote cats' home range size. Thus, we predict that the daily activity pattern of this felid should be additionally shaped by sex and season.

In this study, our goal was to describe Iriomote cat activity patterns and test our predictions concerning its variation relative to sex, reproductive status, and seasonality. By comparing daily activity among different cats during different periods of the year, we aimed to find out if behavioral strategies related to reproduction that were responsible for variation in the cats' movement distances were also effective in shaping their daily rhythm of activity.

Materials and methods

Study area

The study was conducted on Iriomote Island, located at the southernmost end of the Ryukyu Archipelago of Japan (24°20'N, 123°49'E). The area of the island is 284 km² of which 83% is covered by subtropical evergreen forest. The remaining area is occupied by human settlements and agricultural areas, which are restricted to the eastern and northern coasts. The main vegetation type is deciduous forest dominated by *Castanopsis sieboldii* and *Quercus miyagii*. Lowland wetlands are occupied by swampy forest, with *Pandanus odoratissimus*, *Barringtonia racemosa*, and *Cerbera manghas* as the main species. Mangrove forests cover lowlands in estuaries. The interior part of the island is dominated by mountains with a maximum elevation of 469 m asl. The climate is subtropical with a hot summer (April to October, mean temperature: 29°C in July) and a cooler winter (November to March, mean temperature: 17°C in January). The annual rainfall is 2,500 mm. The Iriomote cats inhabit the entire island, however, they likely occur at higher densities in the lowland coastal area than in the mountains (Izawa et al. 2000).

Trapping and radio-tracking

Fifteen individuals (nine males and six females) were captured during two study periods: 1993–1996 and 1999–2001. We captured the cats in box-traps equipped with

radio-alarm systems and baited with live chicks. Once captured, cats were anesthetized by a professional veterinarian with xylazine–ketamine mixture (ketamine hydrochloride 10 mg/kg body weight and xylazine hydrochloride 1.2 mg/kg body weight). The age of cats was determined based on tooth wear, body mass, and signs of lactation in females. The males were considered adults when they weighed >3 kg. The females were considered subadults if they had no previous signs of lactation (Sakaguchi 1994). All animals were fitted with radio-collars (45–70 g; ATS, Isanti, MN, USA, and custom-made by the authors M.O. and N.N.). We radio-tracked cats in three separate study areas: Komi-Otomi on the eastern coast of the island, Funaura in the north, and Shirahama in the west (Fig. 1).

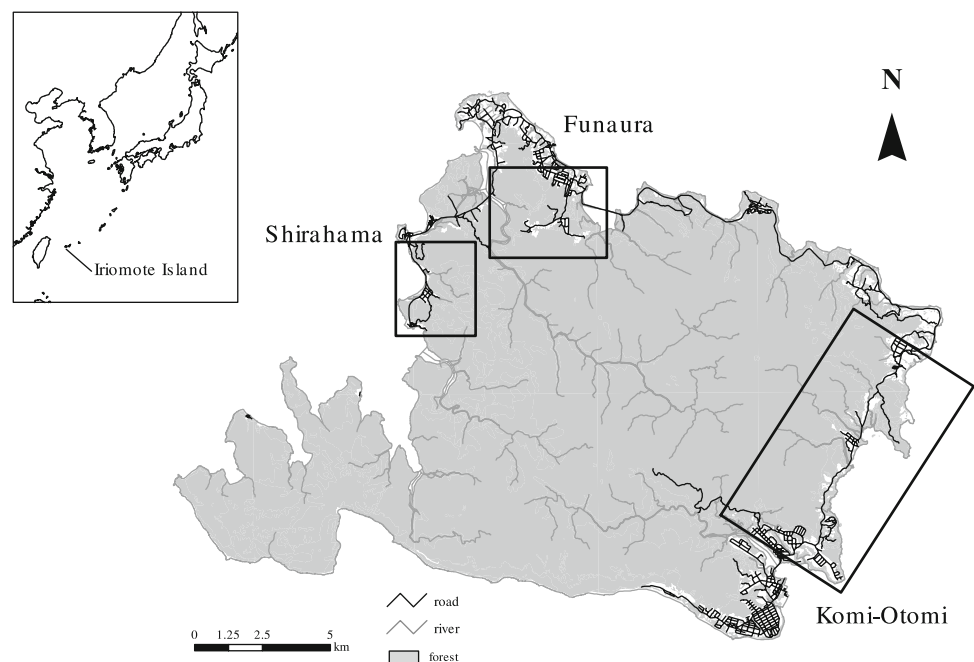
We located the radio-collared cats by triangulation (White and Garrot 1990) from the nearest accessible roads or trails either by car or on foot. The bearings were plotted on a map (1:10,000 with a grid of 500 × 500 m) and locations measured to the nearest 10 m. We did not measure the exact accuracy of radio-fixes in the field due to the inaccessibility of the terrain. However, we could occasionally confirm the accuracy of our radio-locations by sightings of the tagged cats or finding their tracks at a radio-fixed site. Thus we are confident that our accuracy was below the level accepted to determine the cats' activity in this study (see below). To increase the reliability of locations we mainly used those for which three or more bearings intersected at approximately one point when plotted on the map (width of resulting polygon ≤10 m). In cases where locations were less accurate, we excluded

those in which the longest side of the fixed triangle was longer than half the distance between the position of the observer and the furthest apex of the triangle. In the remaining cases, we assumed the position of the animal as the middle of the triangle. When locating moving animals, taking three bearings in time was often not possible, so that such locations were less precise. However, this did not affect the reliability of recording the cat activity as movements were the main index considered in this study.

The range of the transmitters was between 0.1 and 1 km depending on the terrain. While radio-tracking, we tried to maintain a distance of at least 50–100 m from the focal animal to avoid disturbing its natural behavior. On the other hand, occasional sightings of cats suggested that they did not pay much attention to the presence of humans.

We obtained a total of 3,263 readings of the Iriomote cats' activity. We recorded the cats' activity during sessions of radio-tracking lasting from 2 to 24 h/day. These included 57 sessions of continuous radio-tracking that covered the entire 24-h cycle (Appendix). During shorter sessions, recordings were made in different periods throughout the 24-h cycle, so that each time unit (we pooled data into 2-h intervals) was represented by a comparable number of readings (mean ± SD numbers of readings per 2-h interval: 174.5 ± 14.0; 56.6 ± 5.0; 40.8 ± 5.4 for males, breeding females, and non-breeding females, respectively). Consecutive locations were taken every 0.5–1 h. The activity of the cat was recognized based on the change of location from one record to another. We considered the cat active when it moved ≥50 m within a maximum of 1 h. Although we also noted the fluctuation of

Fig. 1 Map of the Iriomote Island (Ryukyu Archipelago, Japan) showing the location of the three study areas



the strength of radio-signals as an index of animals' activity, we did not use it for analysis, as we considered it less reliable than that based on actual movements.

For analysis of seasonal variation in the Iriomote cats' activity we used slightly different periods for males and females, based on the reproductive cycle of the cat (Okamura et al. 2000). The following periods were characterized for males:

1. mating—from November to April (increased rate of urine marking); and
2. non-mating—from May to October.

For females the periods were:

1. nursing—from May to August; and
2. the rest of the year—from September to April.

While adjustment of the analyzed periods separately for each sex allowed their different reproductive activities to be encompassed, the periods distinguished for males and females still largely overlapped, allowing for inter-sexual comparisons in respective seasons. We recognized the reproductive status of females either by radio-tracking data or from photo-trapping. Radio-tracking indicated that a female was breeding when her movements were concentrated around specific sites whereas photo-trapping provided information on the presence of kittens and/or appearance of nipples (Okamura et al. 2000; Okamura 2002).

We tested for differences in patterns of daily activity between cats of different sex and reproductive status and between seasons with the use of the replicated goodness of fit *G*-test. We analyzed the sexual and seasonal variation of duration and number of activity bouts by Kruskal–Wallis one-way analysis of variance, as the data were not normally distributed. In pair-wise comparisons between groups of cats and seasons, we used the Mann–Whitney *U*-test. For large samples ($N > 20$) we used the normal approximation by calculating the standardized *Z*-value of the normal distribution.

Results

General patterns of Iriomote cat activity

The general activity patterns of Iriomote cats showed slightly prevailing activity during the dark periods of the day with particular peaks at dawn and dusk or in the early hours of the night. However, these patterns were clearly dependent on the sex and reproductive status of the cat (Fig. 2). The adult males showed an apparent bimodal pattern of activity with peaks at dawn and in the early hours of the night (at 2000–2100 h). The main phase of their reduced activity occurred during the day (from 800 to 1700 h), whereas the second, shorter one was around

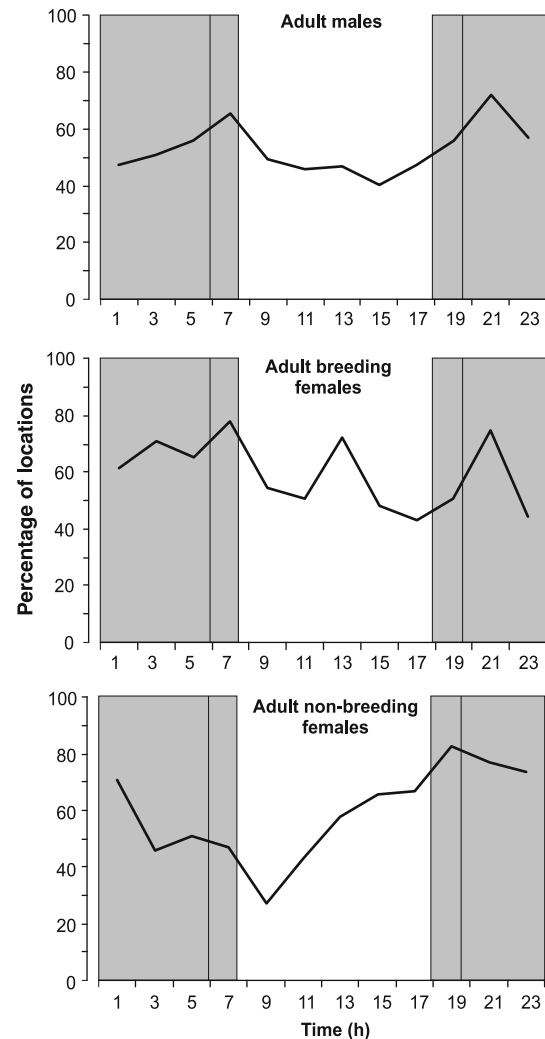


Fig. 2 The activity patterns of Iriomote cats, with division into sex and reproductive status of females (adult males, $N = 9$, adult breeding females, $N = 3$, adult non-breeding females, $N = 5$). Data are pooled in 2-h intervals and expressed as percentages of activity readings recorded when cats moved ≥ 50 m from one location to another within a maximum of 1 h. Gray bars illustrate duration of night with ranges of sunrise and sunset times. Data for non-breeding females include only the non-breeding season (September–April)

midnight. In both low activity phases, however, they were still active $\geq 40\%$ of the time. The adult breeding females had three clear activity peaks with the additional peak around noon (1200–1300 h) (Fig. 2). These patterns were generally not statistically different from each other (replicated goodness of fit test, $G = 10.9$, $P > 0.1$, $df = 11$), however, females were significantly more active than males at 0000–0100, 0200–0300, 0600–0700, and 1200–1300 h in pair-wise comparisons ($G = 4.3$; 8.3; 4.1, and 13.4, respectively; $0.001 < P < 0.05$, $df = 1$). The overall activity pattern of male cats was, however, significantly different from that of non-breeding females ($G = 36.8$, $P < 0.001$, $df = 11$; Fig. 2). The non-breeding females

were also generally active at different times from the breeding ones ($G = 49.8, P < 0.001, df = 11$) with the sole exception of the following times: 0000–0100, 1000–1100, and 2000–2100 h ($G = 1.8; 1.3$ and 0.2 , respectively, $P > 0.1, df = 1$).

The cats moved in 55.2% of radio-locations (pooled for all cats) that is 13.2 h/day. The males were active slightly less (12.7 h) than both breeding and non-breeding females (14.2 and 14.3 h/day, respectively) (Table 1).

Seasonal changes in activity patterns

Males

Adult male Iriomote cats showed significantly different activity patterns between the mating (November–April) and non-mating (May–October) seasons ($G = 28.7, P < 0.01, df = 11$; Fig. 3). During mating they had two peaks of activity, at dawn and early night, whereas during the rest of the year they maintained only one distinct nocturnal peak. The males were active for 11% longer during the mating season (Table 1), however, this difference was not significant ($G = 0.6, P > 0.1, df = 1$). The activity rhythm of males during the mating season generally followed that of breeding females at the same time of the year ($G = 16.1, P > 0.1, df = 11$; compare Figs. 3a and 4b), but not that of non-breeding females ($G = 36.8, P < 0.001, df = 11$; compare Figs. 3a and 2). In the remaining period (May–October), that included the nursing period in females, the activity rhythms of males and breeding females were different ($G = 32.9, P < 0.001, df = 11$; compare Figs. 3b and 4a). Males were then particularly less active than females during nocturnal hours (from 0000 to 0700 h; G values in pair-wise comparisons from 12.2 to 18.3, $P < 0.001, df = 1$) and at the time of the females’ additional midday peak (1200–1300 h; $G = 12.5, P < 0.001, df = 1$).

Females

Breeding female Iriomote cats showed different activity rhythms during the nursing period (May–August)

compared with the rest of the year (kittens’ independence: September–April; $G = 28.0, P < 0.01, df = 11$; Fig. 4). The activity rhythm during the nursing period had an additional conspicuous peak at 1200–1300 h, however, the significant differences between periods occurred only in the morning (0800–0900 hour; $G = 34.6, P < 0.001, df = 1$) and evening hours (1800–1900 and 2000–2100 h; $G = 8.8, P < 0.01$, and $G = 41.5, P < 0.001$, respectively, $df = 1$) with reduced activity during nursing (Fig. 4). Breeding females showed different activity patterns from those of non-breeding females during the period of kittens’ independence ($G = 65.1, P < 0.001, df = 11$). (No activity data were available for non-breeding females in May–August.) Breeding females were more active than non-breeding ones during the late night and morning hours (G from 5.0 to 65.6, $0.001 < P < 0.05, df = 1$), whereas they were less active in the afternoon (1400–1500 and 1600–1700 h; $G = 7.9$ and 8.2 , respectively, $P < 0.01, df = 1$)

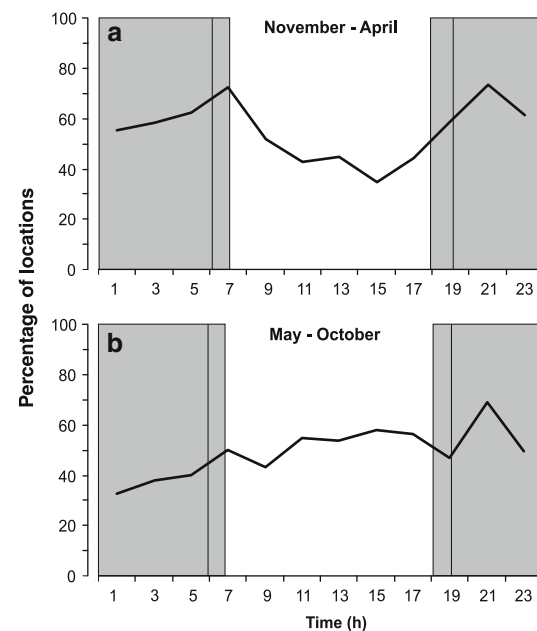


Fig. 3 Seasonal changes in activity patterns of adult male Iriomote cats. a mating season (November–April); b non-mating season (May–October). See Fig. 2 for other explanations

Table 1 Total duration of activity per day in the Iriomote cats, shown as a percentage of active radio-locations (%) and time active in hours (H)

| Cat sex/reproductive status (number of individuals) | Mating/non-nursing season | | | Non-mating/nursing season | | | Whole year | | |
|---|---------------------------|------|-------|---------------------------|------|-----|------------|------|-------|
| | % | H | N | % | H | N | % | H | N |
| Adult males ($n = 9$) | 54.4 | 13.1 | 1,484 | 49.0 | 11.8 | 610 | 52.9 | 12.7 | 2,094 |
| Adult breeding females ($n = 3$) | 64.4 | 15.5 | 264 | 55.9 | 13.4 | 415 | 59.2 | 14.2 | 679 |
| Adult non-breeding females ($n = 5$) | 58.1 | 13.9 | 415 | – | – | – | 59.4 | 14.3 | 490 |

The number of individuals does not equal the total number of radio-tracked individuals as two breeding females (E18 and RR, see Appendix) did not reproduce in one year and were thus scored as both breeding and non-breeding in different years

– denotes lack of data

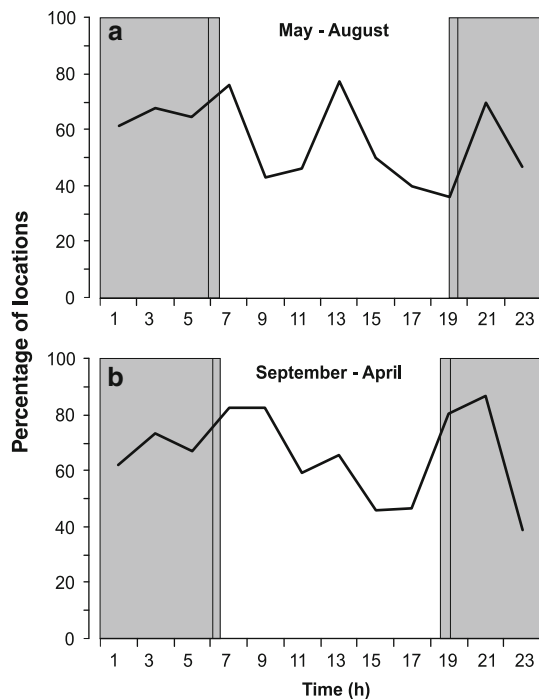


Fig. 4 Seasonal changes in activity patterns of adult breeding female Iriomote cats. **a** nursing season (May–August); **b** non-nursing season (September–April). See Fig. 2 for other explanations

and before midnight (2200–2300 h; $G = 24.9$, $P < 0.001$, $df = 1$).

The total duration of the breeding females' daily activity was 16% shorter (although not significantly: $G = 1.5$, $P > 0.1$, $df = 1$) during the nursing period than at the time of kittens' independence (Table 1). Non-breeding females, on the other hand, in September–April, had a 12% shorter (but also not significantly: $G = 0.8$, $P > 0.1$, $df = 1$) total daily activity than breeding females, which was comparable with that of breeding females in May–August (Table 1).

Variation in activity bouts

The activity of Iriomote cats was characterized by bouts of continuous movements ranging from 0.17 to 9.05 h, alternating with resting bouts (0.25–14.42 h) throughout the day (Table 2). The duration of activity bouts was, however, dependent on the cat's sex and reproductive status and the season of the year (Kruskal–Wallis one-way analysis of variance, $H = 21.36$, $P < 0.001$, $df = 4$). The same factors influenced the duration of resting bouts ($H = 12.65$, $P = 0.01$, $df = 4$), but not the number of bouts ($H = 8.85$, $P = 0.07$, $df = 4$). The longest average (\pm SD) duration of active bouts for breeding females occurred during the period of kittens' independence (3.4 ± 2.8 h), whereas the shortest activity bouts were those of males during the

non-mating season (1.5 ± 1.2). Males had generally shorter average movement bouts than breeding females (1.95 ± 1.7 and 2.69 ± 2.31 h, respectively; Mann–Witney U -test, $Z = -2.79$, $P = 0.005$, $df = 1$). Males were also more frequently active per day than females (but insignificantly; $U = 240$, $P > 0.1$; 5.6 ± 1.8 and 4.9 ± 1.8 , respectively).

During the mating season, the male active and resting bouts were significantly longer ($Z = 3.13$, $P = 0.002$, and $Z = 3.35$, $P = 0.001$, $df = 1$, respectively), and the number of active bouts was fewer ($U = 82.5$, $P = 0.02$, $df = 1$) than during other parts of the year (Table 2). The duration of active bouts of males was shorter than those of breeding females in respective seasons ($Z = -2.28$, $P = 0.02$, and $Z = -2.88$, $P = 0.004$, $df = 1$, for mating and non-mating periods, respectively). In contrast, no difference in the duration of active bouts during the mating (= non-nursing) period was found between males and non-breeding females ($Z = -1.49$, $P = 0.14$, $df = 1$).

Breeding females moved in shorter and more frequent bouts during the nursing period than during other months, although these differences were not significant ($Z = -1.82$, $P = 0.07$, $df = 1$ and $U = 20.0$, $P = 0.08$, $df = 1$, respectively; Table 2). On the other hand, their movement bouts during the non-nursing period were significantly longer than those of non-breeding females ($Z = 2.6$, $P = 0.009$, $df = 1$).

Discussion

Although the daily activity pattern of Iriomote cats varied greatly depending on sex, reproductive status, and season, it can be generally characterized as crepuscular and nocturnal. When compared with available literature data on activity of the cats' main prey species, this pattern seemed to follow the periods of peak activity of prey. The evening peak in cat activity (1900–2100 h) coincided with one of peaks of vocal activity of several amphibian species recorded on the Iriomote island: *Rana supranarina*, *Rhacophorus owstoni*, and *Microhyla ornata* and some orthopteran insects which were found in the cat diet (Watanabe 2003; Watanabe and Kobayashi 2006). The morning peak in cat activity (at 0600–0700 h), however, occurred during a period of high activity of two *Rallidae* bird species that were often hunted by Iriomote cats (*Rallina eurizonoides*, *Amaurornis phoenicurus*; Sakaguchi and Ono 1994, Watanabe 2003, Watanabe and Kobayashi 2006). No published data are available on the daily activity of reptiles, such as skinks, agamids, and snakes (e.g. habu *Trimeresurus elegans*) on the island, that constitute an important part in the Iriomote cat diet (Watanabe 2003). Some reptiles, however, were nocturnal, as indicated by

Table 2 Duration (h) and number of activity bouts (mean \pm SD) of the Iriomote cats

| Activity parameter | Males | | Breeding females | | Non-breeding females |
|----------------------------|---|--|---|--|--|
| | Mating | Non-mating | Nursing period | Non-nursing period | Non-nursing period |
| Duration of active bouts | 2.21 \pm 1.89 (0.33–9.05) <i>163</i> | 1.49 \pm 1.20 (0.17–7.33) <i>93</i> | 2.34 \pm 1.93 (0.50–8.00) <i>51</i> | 3.36 \pm 2.83 (0.42–11.67) <i>26</i> | 1.98 \pm 1.98 (0.37–7.92) <i>40</i> |
| Duration of inactive bouts | 2.01 \pm 2.03 (0.25–14.53) <i>176</i> | 1.46 \pm 1.85 (0.25–14.42) <i>94</i> | 1.80 \pm 1.72 (0.25–9.00) <i>57</i> | 1.56 \pm 1.46 (0.33–6.58) <i>32</i> | 1.90 \pm 2.43 (0.28–10.80) <i>42</i> |
| Number of active bouts/day | 5.17 \pm 1.54 (3–9) <i>29</i> | 6.82 \pm 2.04 (3–9) <i>11</i> | 5.67 \pm 1.37 (4–8) <i>6</i> | 3.75 \pm 1.50 (2–5) <i>4</i> | 6.00 \pm 2.89 (2–10) <i>7</i> |

Minimum and maximum values are given in parentheses. Numbers of locations are in italics. No data were available for non-breeding females during the nursing period

our field observations (Watanabe and Izawa 2002) and by the results of a telemetry study on habu *T. flavorodis* on Amami Island (Wada et al. 1972).

The relationship between the activity of predators and those of its main prey has been suggested by many authors (Curio 1976, Karanth and Sunquist 2000, Scognamiglio et al. 2003), however, the final outcome can be blurred by various factors, such as potential competitive or predatory interactions among coexisting carnivores (Cloudsley-Thompson 1961), hunting strategy, or climate (Hayward and Hayward 2007). In complex ecosystems, detecting the relationship between the predators' and their prey activity rhythm may not be even feasible as it was for the pine marten *Martes martes* in Poland (Zalewski 2001). In some instances, the synchronization of predator and prey activity is not realistic, especially in the case of large carnivores, such as the Eurasian lynx *Lynx lynx*, feeding on ungulates, because the prey is more alert when active (Schmidt 1999). Also, the smallest carnivore, the least weasel *Mustela nivalis*, was found to be active independently of the activity of rodents (their principal prey) as they hunted them in their burrows (Jędrzejewski et al. 2000). The Iriomote cat feeds on small prey and is the only carnivore living on the island, thus it is likely that the coincidence of its activity pattern with those of its main prey is real, as it is not affected by either competition or predation.

Iriomote cats were active for a similar amount of time as previously reported for several populations of another small felid, the leopard cat in the tropical environments of Thailand (i.e. from 47 to 52% of the recorded time: Rabinowitz 1990; Grassman 2000; Grassman et al. 2005; Austin et al. 2007). Ocelots *Leopardus pardalis* also showed a similar level of activity (40–58%: Ludlow and Sunquist 1987; Crawshaw and Quigley 1989). In contrast,

other, larger, cats, such as the Eurasian lynx were active for only 27% of records per day (Schmidt 1999). The lynx usually killed prey larger than themselves (ungulates: Okarma et al. 1997) that provided them with food for several days, which allow long periods of inactivity. Yet lower duration of daily activity was found in feral domestic cats *Felis catus* (20%: Izawa 1983) in Japan, where their population was sustained on an artificial, rich, and permanently available food resource. Thus, the amount of daily activity of predators seems to be related to the type and accessibility of food. A relatively high level of daily activity is likely characteristic for small felids that are dependent upon a variety of natural, yet smaller prey animals (from insects to small mammals: Rabinowitz 1990; Grassman 2000; Watanabe 2003; Ludlow and Sunquist 1987).

Our results showed that besides the effect of prey activity, the circadian rhythm of the activity of Iriomote cats can be explained by factors related to reproduction. It was conspicuous that male cats followed the activity patterns of breeding females only during the mating season, and were not active at the same time as non-breeding ones. This indicates that searching for receptive females could drive male cat activity. The seasonal variation in male activity pattern, including total duration of daily activity and the duration and number of single bouts shown in this research fits very well into the seasonal pattern of movements determined by us in an earlier study (Schmidt et al. 2003). Male cats apparently responded to the changes in their reproductive cycle (Okamura et al. 2000) by accelerating and expanding movements during the mating season. The home ranges of male Iriomote cats overlapped those of females to a similar extent during all seasons (Sakaguchi 1994), however, their core areas overlapped extensively only during mating, which was when close

encounters also occurred between them (Okamura 2002). These findings are in accordance with the prediction by Sandell (1989) that the reproductive tactics of males and females of solitary carnivores should influence their use of space in different ways.

Peculiarities of female Iriomote cat activity pattern can be also clearly explained in light of Sandell's (1989) prediction. He predicted that, in contrast to males that rely on access to females, it is food availability and distribution that determines female reproductive success. This is because female solitary carnivores are solely responsible for providing food for their offspring. Indeed, in this study, only the breeding female Iriomote cats showed an additional mid-day peak of activity. Moreover, this peak was only clear during the nursing period. It is reasonable to assume that during the day lactating females have to frequently move to and from the den site to nurse kittens and obtain sufficient food to sustain themselves, and at a later stage to provide solid food for kittens (Okamura 2002). This increased activity pattern was also seen in shorter but more frequent activity bouts per day during nursing than at the time of kittens' independence. It may seem, however, surprising that the general level of breeding females' activity was lower during nursing than at other times. On the other hand, it must be noted that the nursing time coincides with the period of highest food availability on the island (Sakaguchi 1994, Watanabe et al. 2005). Thus, females may not need to go far from kittens to satisfy their energy needs—they leave kittens often, but only for a short time. Indeed, the daily ranges of female movements were smallest during that period (Schmidt et al. 2003). Also, the high food availability could allow cats to forage very close to the dens, so that some movements within a radius of 50 m from the den may not have been detected. On the other hand, the overall longer time of females' activity during the period of kittens' independence may be due to two reasons. First, it is likely that a lower food abundance resulted in the need to travel farther in search for prey—the daily movement ranges were then, indeed, larger relative to nursing time (Schmidt et al. 2003). The second reason, however, could be the greater energy needs of females recovering after the exhausting period of lactation. The fact that non-breeding females were less active than breeding ones at that time may also support this latter assumption.

Previous data on seasonal changes in activity levels of the closely related leopard cat (Rabinowitz 1990; Grassman 2000; Grassman et al. 2005; Austin et al. 2007) provided somewhat contradictory results to ours showing either a lack of seasonal change or lower activity during the cooler (dry) season. It is, however, worth noting that in

those studies the data for all cats were pooled for analyses and no information were given about their reproductive status. Our research emphasized great variability in activity patterns related to sex and reproductive status of the cats.

The daily activity of small carnivores can also be substantially influenced by ambient temperature, as was shown by Zalewski (2000) for pine marten in Poland, which dramatically reduced their activity time during the non-breeding period (winter), despite a simultaneous decrease in food abundance. In that study, however, there were severe differences in average monthly temperatures between the warm (22.5°C) and cold (−8.5°C) seasons (Zalewski 2000). A significant negative influence of temperature on activity patterns was also found for feral domestic cats (Izawa 1983). Because of the relatively low seasonal variation of temperatures on Iriomote Island, the results obtained in our research were more likely to discern the effect of reproductive status of the cat on its activity.

Since the publication of Sandell's (1989) theory on the influence of different mating tactics on the spacing patterns of male and female solitary carnivores, there has been an increasing amount of empirical evidence that reproductive strategies have an even wider influence on animal behavior. Besides its apparent effect on space use in various predators (Sakaguchi 1994; Schmidt et al. 1997; Kovach and Powell 2003; Baghli and Verhagen 2004; Herfindal et al. 2005), reproductive strategies have been found to influence activity patterns in the Eurasian lynx (Schmidt 1999) and pine marten (Zalewski 2000, 2001). Such effects were also shown for movement patterns of the lynx (Jędrzejewski et al. 2002) and Iriomote cats (Schmidt et al. 2003). These studies documented that, indeed, different reproductive strategies of male and female solitary felids are clearly seen in their various life-history traits. Our present study has contributed to this knowledge by providing information on the Iriomote cat activity that was not previously available and revealing its sexual and seasonal variability. However, due to a limited sample size our results should be treated as tentative and more research is still needed to provide further evidence on this issue.

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Appendix

Adult Iriomote cats radio-tracked for a study of activity patterns from 1993 to 2004, Iriomote Island, Japan

| Cat's ID | Sex | Time of monitoring | Number of locations | Number of 24-h radio-tracking sessions |
|----------|-----|----------------------------------|---------------------|--|
| RR* | F | 6 November 1993–21 October 1996 | 83 | – |
| BB | F | 6 November 1993–7 November 1995 | 61 | – |
| SN | M | 9 March 1995–17 October 1996 | 10 | – |
| W-60 | F | 5 March 1999–6 November 1999 | 125 | 2 |
| E-18* | F | 4 June 1999–22 October 2000 | 348 | 6 |
| E-30 | M | 28 August 1999–9 November 2004 | 555 | 5 |
| E-36 | F | 18 October 1999–22 October 1999 | 48 | – |
| E-33 | M | 31 October 1999–22 December 2001 | 83 | – |
| Omo | M | 20 June 2000–29 July 2000 | 94 | 1 |
| Oki | M | 29 June 2000–2 December 2000 | 103 | 1 |
| Yonku | M | 15 June 2000–8 March 2001 | 1,118 | 33 |
| Nene* | F | 26 June 2000–15 February 2001 | 504 | 9 |
| W-89 | M | 21 November 2001–5 March 2002 | 39 | – |
| W-86 | M | 22 November 2001–31 January 2002 | 57 | – |
| W-81 | M | 24 November 2001–6 March 2002 | 35 | – |

An asterisk indicates female reproducing during at least one year of the study period

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