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Abstract: Movement pattern of the Iriomote cat *Prionailurus bengalensis irimotensis* was studied on Iriomote Island, Japan by radio-tracking. The influence of sex and reproductive status of cats on their daily movement distance (DMD), straight-line distance (SLD), daily movement range (DMR) and other relative indices of movements was estimated. DMD was longest in males (3.2 km) and shortest in females without kittens (1.9 km). Also, males moved faster than either females with or without kittens (0.34, 0.25 and 0.25 km/h, respectively). During the mating season, males moved faster and their DMRs were larger than during the rest of the year. The SLD/DMD ratio in males was similarly high in both seasons (0.29 and 0.33), which indicates that their daily routes were expanded over large areas year-round, possibly to maintain a continuous control over their home range. In contrast, SLD/DMD varied seasonally in breeding females. It was low (0.09) during the lactating period, when females returned repeatedly to the den with kittens and it became high (0.32) out of the breeding season. Breeding females moved equally long DMDs in both seasons, whereas non-breeding ones moved shorter distances during the breeding period. These differences may be related to seasonal changes of food abundance. Cats moved intensively, as indicated by long (812-1139 m) routes per km² of their home range, and occasionally visited distant parts of their ranges in a short time (4-5 days). On the other hand, they showed a relatively slow increase of the patrolled area, from 10% to 36% of their home ranges, in the first and fifth day, respectively. Movement pattern of Iriomote cats showed no clear relation to active defence of home ranges.

Movements and use of home range in the Iriomote cat (*Prionailurus bengalensis iriomotensis*)

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Abstract

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Key words: Iriomote cat, home range, behaviour, reproductive strategy, territoriality, *Prionailurus bengalensis iriomotensis*

INTRODUCTION

The Iriomote cat *Prionailurus bengalensis iriomotensis* is endemic to Iriomote Island, in the Ryukyu Archipelago in Japan. Due to the inaccessibility of the forest that the cats occupy (dense vegetation, lack of roads) and to the remoteness of the island, they remained unknown to science until 1965 (Imaizumi, 1967). Although the Iriomote cats are morphologically (Leyhausen & Pfeleiderer, 1999) and ecologically (Sakaguchi, 1994) unique in relation to other small cats of south-east Asia and were long considered a separate species, their specific distinction has been recently questioned by molecular methods (Masuda *et al.*, 1994; Johnson *et al.*, 1999). The biology and ecology of Iriomote cats has been studied

by means of faecal analysis, telemetry and photo-trapping (e.g. Imaizumi, Imaizumi & Tyabata, 1976; Yasuma, 1981; Ikehara & Konishi, 1983; Izawa, Doi & Ono, 1991; Sakaguchi, 1994; Sakaguchi & Ono, 1994). Nevertheless, some aspects of their life history, such as movement patterns, have not yet been described.

In general, the mobility of animals is related to foraging, social contacts and the search for sexual partners. Thus, detailed studies on movement patterns are essential to our understanding of social and spatial organization. On the other hand, determining movement routes of cats in the wild, either by snow-tracking or radio-tracking, is labour intensive, so this aspect of felid biology still remains little known. In their recent study on the Eurasian lynx *Lynx lynx*, Jędrzejewski *et al.* (2002) hypothesized that the rate of movements in felids is relatively constant and strongly affects the defensibility of their territories. As scent-marking is a source of individual advertisement and avoidance of conspecifics in cats (Mellen, 1993),

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felids may not be able to control the entire territory and discourage intruders if a home range exceeds some threshold in size. The lynxes used large home ranges (130 and 250 km², in females and males, respectively; Schmidt, Jędrzejewski & Okarma, 1997) and yet moved little (7 km/day, on average), so they probably could not patrol it regularly. The Iriomote cats, as representatives of small-sized felids living in a rich subtropical forest, use small home ranges (1.8 and 3.0 km², in females and males, respectively; Izawa, Doi *et al.*, 1991). The extent of their movements should enable them to maintain a continuous and efficient control over their territory.

Mating and breeding in the Iriomote cats was not restricted by season, but the peak of mating activity fell between February and April, and parturition occurred mainly from April to June (Okamura *et al.*, 2000). Based on the seasonal dynamics of the home ranges of cats, Sakaguchi (1994) has suggested that the spacing pattern of females is food related, whereas access to females determines spacing for the males. In the Eurasian lynx, both spacing pattern and daily activity and movements differ between males and females (Schmidt *et al.*, 1997; Schmidt, 1999; Jędrzejewski *et al.*, 2002). We predicted that movements of the Iriomote cats would also exhibit variation related to reproduction: males should move more extensively during the mating season, and the movements of females should be restricted by rearing kittens.

The aim of our study was to describe the characteristics of Iriomote cat movements by measuring: daily movement distance, straight line distance, speed of movement, and range of daily movements. An attempt was also made to estimate the rate at which the cats use their home ranges in order to determine their efficiency in patrolling it. The seasonal variation of movements in males and females were analysed to test for differences in their reproductive strategies.

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 of the island is dominated by mountains with a maximum elevation of 469 m a.s.l., and they are inaccessible to people. The climate is subtropical with a hot summer (April–October, with a mean temperature of 29 °C in July), and a cooler winter (November–March, with a mean of 17 °C in January). The annual rainfall is 2500 mm. The Iriomote cats occur throughout the island, but their densities are probably higher in the lowland

coastal area than in the mountains (Izawa, Sakaguchi & Doi, 2000).

MATERIAL AND METHODS

Overall, 11 individuals (5 males and 6 females) were captured during 2 separate periods from 1993 to 1996 and from 2000 to 2001. For the captures, box-traps equipped with radio-alarm systems and baited with live chicks¹ were used. Once captured, cats were anaesthetized by a professional veterinarian with xylazine–ketamine mixture (ketamine hydrochloride 10 mg/kg body weight and xylazine hydrochloride 1.2 mg/kg body weight). All animals were fitted with radio-collars (ATS Inc., Isanti, Minnesota, U.S.A., and custom-made by two of us: MI and NN). Cats were radio-tracked in 3 separate study areas: Komi-Otomi on the eastern coast of the island, Funaura in the north, and Shirahama in the west.

Movements of the radio-collared cats were monitored continuously for 1- to 7-day periods, by car or on foot. Locations were taken by triangulation (White & Garrot, 1990) from a minimum of 3 points (marked with GPS) on the roads or trails. They were later plotted on a map (1:10 000 with a grid overlay, corresponding to 500 × 500 m) and measured to the nearest 10 m. It was not possible to test the accuracy of radio-locations in the field owing to the inaccessibility of the terrain. However, the main locations used were those for which 3 or more bearings intersected at 1 point when plotted on the map. Occasionally, the accuracy of radio-locations could be confirmed by sightings of cats or by finding their tracks at a radio-fixed site. Where bearings failed to determine an exact point, those in which the longest side of the fixed triangle was longer than half the distance between the position of the observer and the farther apex of the triangle were excluded. In the remaining cases, the position of the cat was assumed to be in the middle of the triangle. To increase our confidence concerning the accuracy of locations, most fixes determined with only 2 bearings were excluded. However, such fixes were used when the cat was moving, because it was not possible to take 3 bearings in time.

The range of transmitters was between 0.1 and 1 km depending on the terrain. During radio-tracking, a distance of at least 50–100 m to the focal animal was maintained to avoid disturbing its natural behaviour. Occasional sightings of the cats indicated that they did not pay much attention to the presence of humans.

A total of 3509 locations on all cats was obtained, including 147 sessions of continuous 24-h radio-tracking (Appendix). The movements of the cats were characterized by calculating the following parameters:

(1) *daily movement distance* (DMD): the sum of straight line distances between consecutive locations

¹ The use of live animals as bait is not allowed under U.K. Home Office legislation.

Table 1. Movement characteristics of the Iriomote cat *Prionailurus bengalensis iriomotensis*. DMD, daily movement distance; SLD, straight-line distance; DMR, daily movements range; DMR%, daily movements range as a percentage of the total home range; IM, index of intensity of movements. Values are mean \pm SD and range. Results of Mann–Whitney *U*-test are pairwise comparisons between males and females with kittens (U_1, P_1), males and females without kittens (U_2, P_2) and females with and without kittens (U_3, P_3)

Movements	Adult males (<i>n</i> = 5)	<i>n</i>	Females with kittens (<i>n</i> = 2)	<i>n</i>	Females without kittens (<i>n</i> = 4)	<i>n</i>	Mann–Whitney <i>U</i> -test					
							U_1	P_1	U_2	P_2	U_3	P_3
DMD (km)	3.24 \pm 1.02 (1.47–6.11)	53	2.24 \pm 0.95 (0.63–4.65)	63	1.89 \pm 0.77 (0.18–3.71)	31	2557.0	<0.001	1425.0	<0.001	1158.0	0.144
SLD (km)	1.0 \pm 0.90 (0.04–3.67)	63	0.55 \pm 0.52 (0.01–1.96)	68	0.63 \pm 0.40 (0.06–1.74)	37	2890.0	0.001	1375.5	0.134	1003.5	0.09
DMR (km ²)	0.50 \pm 0.46 (0.08–2.21)	58	0.24 \pm 0.24 (0.01–1.41)	78	0.19 \pm 0.13 (0.002–0.60)	45	3308.5	<0.001	2052.0	<0.001	1759.0	0.983
DMR%	12.49 \pm 8.88 (1.70–38.31)	58	8.91 \pm 7.43 (0.50–35.15)	78	11.22 \pm 8.55 (0.10–38.20)	45	2906.5	0.005	1400.0	0.525	1390.5	0.056
IM (m/km ²)	1075.23 \pm 370.10 (535.22–2217.50)	38	812.20 \pm 167.76 (511.62–1162.38)	20	1139.90 \pm 398.64 (651.90–1982.89)	10	554.0	<0.005	167.0	0.559	48.0	0.02
Speed (m/h)	341.20 \pm 139.66 (144.00–748.00)	49	246.95 \pm 113.60 (94.00–487.00)	20	245.10 \pm 83.35 (155.00–393.00)	10	694.5	<0.01	351.0	0.032	91.0	0.692

Table 2. Seasonal changes in movement parameters of male Iriomote cats *Prionailurus bengalensis iriomotensis*. See Table 1 for abbreviations

Movement	Non-mating period (May–Oct)	<i>n</i>	Mating period (Nov–Apr)	<i>n</i>	Mann–Whitney <i>U</i> -test	
					<i>U</i>	<i>P</i>
DMD (km)	3.12 \pm 1.03 (2.16–5.60)	14	3.29 \pm 1.03 (1.47–6.11)	39	235.0	0.443
SLD (km)	1.0 \pm 0.88 (0.14–3.06)	21	0.99 \pm 0.91 (0.04–3.67)	42	426.0	0.827
DMR (km ²)	0.42 \pm 0.41 (0.09–1.28)	16	0.54 \pm 0.47 (0.08–2.21)	42	238.5	0.09
DMR%	8.87 \pm 6.36 (3.12–22.07)	16	13.88 \pm 9.37 (1.70–38.31)	42	206.5	< 0.05
IM (m/km ²)	896.24 \pm 180.57 (575.61–1163.40)	11	1148.15 \pm 404.10 (535.22–2217.50)	27	89.0	0.055
Speed (m/h)	271.60 \pm 107.18 (189.00–554.00)	10	359.05 \pm 142.53 (144.00–748.00)	39	276.0	< 0.05

during continuous 24-h radio-tracking sessions lasting from noon to noon;

(2) *straight line distance* (SLD): between single locations taken in consecutive days around noon;

(3) *the ratio SLD/DMD*: calculated to describe variation in the movement manner in particular groups of cats; it could theoretically range from 0, when the animal returns to the same place after 24-h to 1 if the animal moved along a straight line;

(4) *daily movement range* (DMR): the area encompassing the daily movement route;

(5) *daily movement range as a percentage of a total home range* (THR: annual 100% minimum convex polygon, based on all locations collected during a given year of radio-tracking) (DMR%);

(6) *the intensity of movements* (IM), after Goszczyński (1986): length of the route (m) the cat moved per 1 km² of its total home range per day, calculated as DMD/THR (for the period 2000–2001 only; see below); this index

describes how intensively cats searched their home ranges – it shows if the daily routes were concentrated or loosely distributed;

(7) *speed of travel*: calculated as a distance moved/h based on 79 periods of radio-tracking lasting from 1 to 8.5 h when cats moved continuously.

Locations were taken every 1–4 h for all cats in 1993–96, and at 0.5- to 1-h intervals for all cats except 1 during 2000–01 (Appendix). Because the area used by cats was not fully accessible, contact with radio-tracked animals was often lost. Therefore, calculation of DMD and IM was excluded on those days when cats could not be located for a continuous period of > 4 h. These days were used, however, for calculation of SLD and DMR. Samples from both study periods were pooled for calculation of movement parameters, because no consistent differences were found between them when they were calculated separately.

On 3 occasions, a cat's movements were monitored by direct observation. These observations were possible because the animal was moving along the edge of the forest and a rice field. The rice was freshly planted and the grass around the field was cut. Observations occurred either at night or in the twilight. The cat was followed with use of spotlight and binoculars. A reflective tape on the radio-collar facilitated observation. The distance between the observer and the cat was 50–100 m.

Seasonal variation of movement parameters was analysed in slightly different periods for males and females, based on the observations of the reproductive cycle of the Iriomote cats (Okamura *et al.*, 2000). The following periods were characterized for males: (1) mating, from November to April (increased rate of urine marking); (2) non-mating, from May to October; and for females: (1) nursing, May–August; (2) rest of the year, September–April.

The basic movement parameters were calculated with the program TRACKER (A. Angebjörn Radio Location Systems AB, Huddinge Sweden). The sexual and seasonal variation of particular parameters were tested with Kruskal–Wallis 1-way analysis of variance. For pairwise comparisons between groups of cats and seasons, the Mann–Whitney *U*-test was used because the data were not normally distributed.

RESULTS

General characteristics of movements of the Iriomote cat

All basic movement characteristics of the Iriomote cats varied significantly among cats of different sex, reproductive status and between seasons (Kruskal–Wallis one-way analysis of variance: DMD, $H = 44.0$, d.f. = 5, $P < 0.001$; SLD, $H = 50.1$, d.f. = 5, $P < 0.001$; DMR, $H = 47.3$, d.f. = 5, $P < 0.001$; DMR%, $H = 25.3$, d.f. = 5, $P < 0.001$; IM, $H = 14.2$, d.f. = 4, $P < 0.01$; speed, $H = 12.9$, d.f. = 4, $P = 0.01$) (Tables 1–3).

The cats moved an average of 2.5 km/day. The DMD varied, however, from 0.18 km in females without kittens to 6.11 km in males. Males moved significantly longer daily distances (DMD) than females, either with and without kittens (Table 1). Breeding females moved similar DMDs to non-breeding ones. The distances between locations taken at 24-h intervals (SLD) were 70% shorter, on average, for all cats. It ranged from 0.01 km in reproducing females to 3.67 km in males. On average, the SLD was longest in males (almost twice as long as in females) and no difference was found between females with and without kittens.

On average, the daily movements of all cats pooled covered an area 0.3 km² (DMR), which comprised *c.* 10% of the mean total home-range size. The DMR% was largest in males and smallest in females with kittens (Table 1). Non-reproducing females covered larger daily ranges than reproducing ones, though the difference was not significant. All cats showed high intensity of movements (IM), with an average of about 1 km of travel route/km² of

Table 3. Seasonal changes in movement parameters of female Iriomote cats *Prionailurus bengalensis iriomotensis*. Lactation, May–August. See Table 1 for other explanations

Movement	Females with kittens			Females without kittens			Mann–Whitney <i>U</i> -test				
	Nursing	<i>n</i>	Rest of the year	Nursing	<i>n</i>	Rest of the year	<i>U</i>	<i>P</i>	<i>P</i>		
DMD (km)	2.18 ± 0.95 (0.85–4.65)	34	2.33 ± 0.97 (0.63–4.02)	1.29 ± 0.52 (0.72–2.37)	8	2.10 ± 0.74 (0.18–3.71)	430.5	0.389	23	25.0	< 0.005
SLD (km)	0.21 ± 0.23 (0.01–0.88)	34	0.88 ± 0.52 (0.05–1.96)	0.54 ± 0.44 (0.14–1.52)	8	0.65 ± 0.40 (0.06–1.74)	116.5	< 0.001	29	87.5	0.293
DMR (km ²)	0.15 ± 0.14 (0.01–0.55)	37	0.31 ± 0.28 (0.01–1.41)	0.11 ± 0.11 (0.02–0.45)	12	0.22 ± 0.13 (0.002–0.59)	477.5	0.005	33	72.0	0.001
DMR%	6.72 ± 5.35 (0.60–26.00)	37	10.89 ± 8.49 (0.50–35.15)	7.79 ± 7.58 (1.40–30.60)	12	12.46 ± 8.64 (0.1–38.20)	541.5	< 0.05	33	93.0	< 0.01
IM (m/km ²)	898.61 ± 187.40 (540.60–1162.38)	7	765.68 ± 142.48 (511.62–1005.00)	–	–	1139.90 ± 398.64 (651.90–1982.89)	70.0	0.052	10	–	–
Speed (m/h)	244.57 ± 114.99 (94.00–376.00)	7	248.23 ± 117.55 (130.00–487.00)	–	–	245.10 ± 83.35 (155.00–393.00)	43.0	0.843	10	–	–

Table 4. Average overlap between consecutive daily movement ranges (DMR) of the Iriomote cats. Season 1, November–April (mating) in males and May–August (nursing) in females; season 2, May–October in males and September–April in females. See Table 1 for other explanations

Sex/reproductive status	Annual average	<i>n</i>	Season 1	<i>n</i>	Season 2	<i>n</i>
Adult males	31.87 ± 26.79 (0.00–99.20)	36	36.35 ± 28.36 (0.09–99.20)	27	18.42 ± 15.96 (0.00–41.30)	9
Females with kittens	27.07 ± 26.93 (0.00–99.70)	53	38.99 ± 28.18 ^a (0.00–99.70)	28	13.71 ± 18.07 ^a (0.00–72.50)	25
Females without kittens	21.82 ± 24.26 (0.00–79.30)	25	17.15 ± 21.14 (0.00–46.20)	4	22.71 ± 25.18 (0.00–79.30)	21

^a Different from another season (Mann–Whitney *U*-test, $U = 563.0$, $n < 0.001$).

the home range. The IM was significantly lower in females with kittens in comparison to males and non-reproducing females (Table 1).

The average speed of Iriomote cats based on radio-tracking was 305 m/h. Males moved significantly faster than females (Table 1). Reproducing and non-reproducing females moved at similar rates. The maximum speed recorded between two radio-locations of a male, confirmed by sightings separated with a 25-min interval (thus, not included in average) was 972 m/h in January 2001.

The index SLD/DMD was highly variable among groups of cats and seasons (Kruskal–Wallis one-way analysis of variance: $H = 49.4$, d.f. = 5, $P < 0.001$). It was lowest in females with kittens (0.20 ± 0.16) and highest in females without kittens (0.33 ± 0.18) (Fig. 1). Males and females without kittens had similar SLD/DMD ratios.

Seasonal variation in movement patterns

The daily movements of males during the mating season covered a 56% larger portion of their home ranges (DMR%), as compared to the rest of the year. Males also moved 32% faster during the mating period. In contrast, other parameters of male movements (DMD, SLD, DMR, as well as SLD/DMD ratio) did not change significantly between seasons (Table 2, Fig. 1). A relative increase of 28% in the intensity of movements (IM) during mating was observed in males, though its significance was weak.

Seasons strongly influenced movement parameters in females with kittens (Table 3, Fig. 1). The SLD was 76% shorter, the DMR and DMR% were 52% and 38% smaller, respectively, during the nursing period in comparison to another season. The SLD/DMD ratio was particularly small in May–August (0.09 ± 0.09) in comparison to September–April (0.32 ± 0.13). During the latter period, it seemed to be at the same level as for the non-reproducing females and males in November–April (Fig. 1). On the other hand, the DMDs and the speed of movements in females with kittens remained unchanged during the year.

Females without kittens showed a somewhat reversed pattern of seasonal variation in movements, when compared to reproducing females (Table 3). Their DMD was 39% shorter during May–August than in September–April. During the latter period, they moved distances as long as those of reproducing females throughout the year. Unlike females with kittens, their SLD as well as

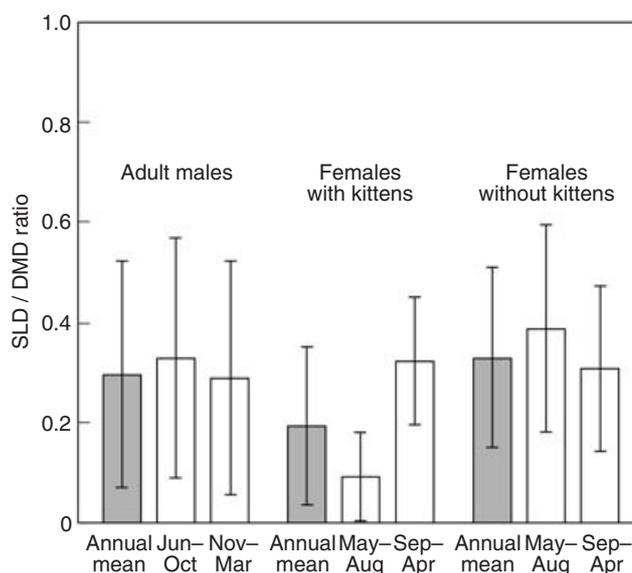


Fig. 1. Average ratios (annual and seasonal means ± SD) of a straight line distance between daily locations (SLD) to an actual daily movement distance covered by Iriomote cats *Prionailurus bengalensis iriomotensis*. Differences between groups of cats and seasons were calculated with Mann–Whitney *U*-test for pairwise comparisons (adult males vs females with kittens, $U = 2071$, $N_1 = 52$, $N_2 = 63$, $P < 0.05$; females with kittens vs females without kittens, $U = 546$, $N_1 = 63$, $N_2 = 31$, $P = 0.001$; nursing period (May–August) vs rest of the year (September–April) in females with kittens, $U = 72$, $N_1 = 34$, $N_2 = 29$, $P < 0.001$).

the SLD/DMD ratio, remained similar in both periods (Table 3, Fig. 1) (SLD: 0.5 and 0.7 km, respectively; SLD/DMD: 0.39 and 0.31, respectively). However, the range of their movements (DMR and DMR%), similarly to that of reproducing females, was significantly smaller (by 50% and 37%, respectively) during the nursing period.

The pattern of home range use

Movement routes of the cats during a single day covered various portions of their total home range, ranging from < 1% to 38%. The average cumulative percentage area used by cats during 5 consecutive days increased up to $36 \pm 12\%$ (20–49%) in males, and $35 \pm 14\%$ (21–56%) in non-reproducing females (Fig. 2). Females with kittens

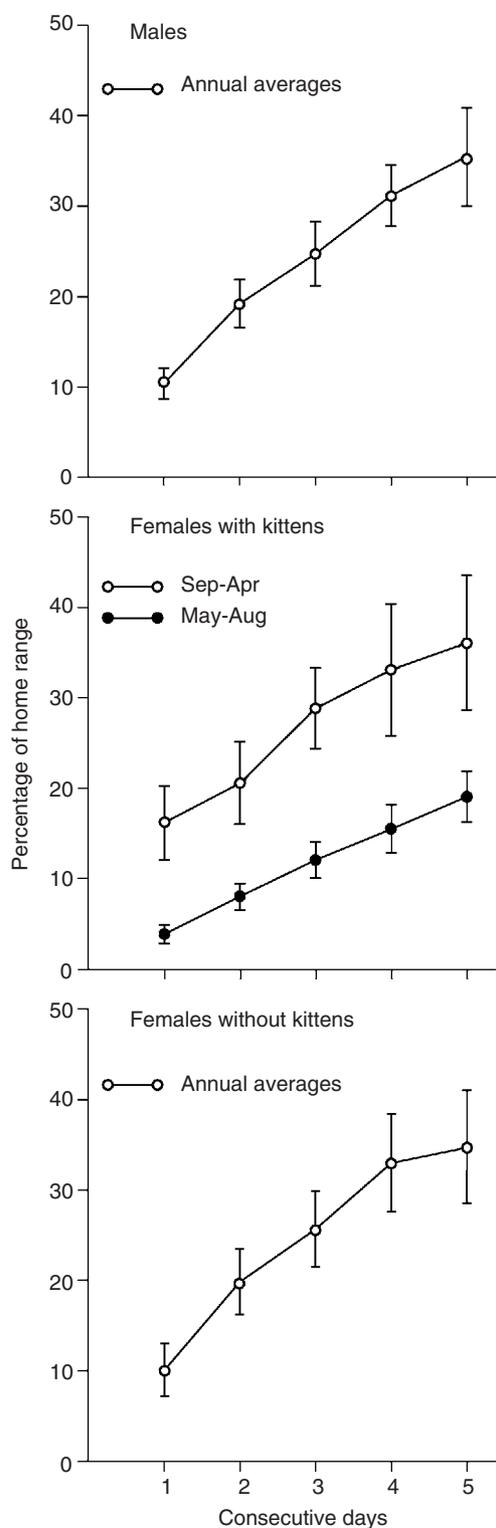


Fig. 2. Increase of home-range use by Iriomote cats *Prionailurus bengalensis iriomotensis*: cumulative area of five consecutive daily movement ranges (DMR means \pm SD) shown as percentage of total home-range size (males, $N_1 = 14$, $N_2 = 9$, $N_3 = 8$, $N_4 = 9$, $N_5 = 5$; females with kittens, $N_1 = 18$, $N_2 = 15$, $N_3 = 15$, $N_4 = 10$, $N_5 = 9$; females without kittens, $N_1 = 10$, $N_2 = 9$, $N_3 = 8$, $N_4 = 6$, $N_5 = 6$). Samples were sufficient for seasonal comparisons in females with kittens only. Differences between groups of cats and seasons were calculated with Mann–Whitney U -test for pairwise comparisons.

used their ranges at a similar rate to males and non-reproducing females from September to April only. Then the cumulative area of five consecutive DMR increased up to $36 \pm 17\%$ (13–59%) of their total home ranges. During a nursing period, however, it reached only $19 \pm 6\%$ (13–26%) in a fifth day of radio-tracking (Fig. 2).

The average overlap between each consecutive DMR was $27 \pm 26\%$ for all cats, with extremes between 0% and 100%. There was substantial variation in the extent of overlapping DMR among cats of different sex, reproductive status and seasons (Kruskal–Wallis one-way analysis of variance: $H = 19.7$, d.f. = 5, $P = 0.001$) (Table 4). However, the only significant difference in pairwise comparisons was found between seasons in reproducing females, with the overlap being bigger during the nursing period (Table 4). In females without kittens, in contrast, the overlap was smaller (though not significantly) during the nursing period than in September–April. In males, consecutive DMR overlapped more during the mating season than during the rest of the year.

To find out if the cats showed any avoidance of using the same area on consecutive days, the percentage of overlap was compared between the first and each of the subsequent DMRs. In males and females with kittens, a regular increase of the overlapping percentage in subsequent days (Fig. 3) was found, although it was not significant (males, $H = 6.5$, d.f. = 5, $P = 0.265$; females, during the nursing period, $H = 3.9$, d.f. = 4, $P = 0.417$; females, non-nursing period, $H = 5.6$, d.f. = 3, $P = 0.135$). Thus, there was no clear threshold in repeated use of the previous area, but rather a steady increase of an overlapping area. In general, overlapping of the first DMR by each of subsequent DMRs was relatively high. In males, the area used on day 1 was overlapped by 21–32% with the next three DMRs, and it increased up to 66% on day 7. In females with kittens, high overlap (from 33% to 47%) between DMR 1 and three subsequent DMRs occurred during the nursing period only (Fig. 3). In other seasons, it was usually $< 10\%$. The overlap in non-reproducing females was low, but the changes in subsequent days were irregular (Fig. 3).

Occasionally, the cats moved so their routes encompassed most of their home range in 4 or 5 consecutive days, regardless of sex or reproductive status (Fig. 4). Only females with kittens during the nursing period concentrated their movements near the den.

Direct observations of movements

One radio-collared adult male was observed three times for longer periods (60, 54 and 5 min, respectively). On 21 February 2001, the cat was observed almost

Significant differences were found in females with kittens only between seasons in days 1, 2, 3 and 4 ($U = 17$, $N_1 = 8$, $N_2 = 10$, $P < 0.05$; $U = 9$, $N_1 = 7$, $N_2 = 8$, $P < 0.05$; $U = 7$, $N_1 = 6$, $N_2 = 9$, $P < 0.05$; $U = 3$, $N_1 = 5$, $N_2 = 5$, $P < 0.05$, respectively).

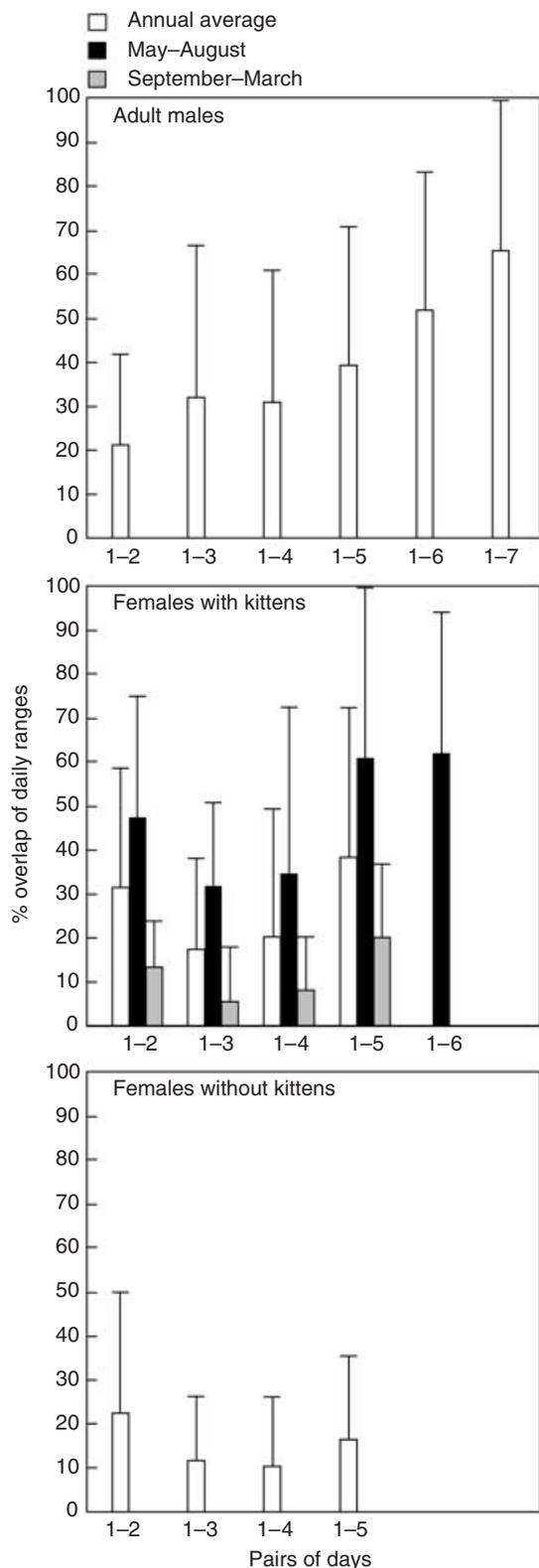


Fig. 3. Percentage overlap (mean \pm SD) between the first and each of subsequent consecutive daily movement ranges (DMR) in Iriomote cats *Prionailurus bengalensis iriomotensis* (males, $N_1 = 8, N_2 = 8, N_3 = 11, N_4 = 4, N_5 = 5, N_6 = 4$; females with kittens, $N_1 = 15, N_2 = 16, N_3 = 11, N_4 = 9, N_5 = 5$; females without kittens, $N_1 = 9, N_2 = 8, N_3 = 6, N_4 = 6$). Samples were sufficient for seasonal comparisons in females with kittens only. Differences between

continuously between 04:30 and 05:30. During this period, he moved 358 m, so that his speed was 358 m/h. However, during half this time, the animal stayed at one place, sitting and watching. During 15 min, he more or less uninterruptedly walked 95 m, making short breaks for hunting (chasing, pouncing or pawing in water) and eating, travelling at a speed of 380 m/h. For comparison, if calculated with three single locations at 30 min intervals during the whole observation period, the distance moved by this cat, was only 291 m. On 22 February 2001, this same animal was observed between 22:06 and 23:00. During this period, he moved 238 m, at a speed of 264 m/h. His travel was interrupted with two 10–15 min breaks for eating, so that his actual speed during continuous movements was: 1860, 720 and 816 m/h. The distance moved according to three locations taken every 30 min was 175 m. On 7 March 2001, the same cat was observed walking between 06:40 and 06:45. He traversed 90 m, so that his actual speed was 1080 m/h.

DISCUSSION

The daily movement distances of the Iriomote cats certainly do not reflect the actual distance moved by these cats. According to visual observations, the DMD calculated from standard locations taken with 30-min intervals was underestimated by 19–27%. Therefore, movement characteristics resulting from radio-tracking represent minimum values. Estimated speed of movement, on the other hand, seems to reflect the typical velocity of Iriomote cats. Although they were able to move at a speed of *c.* 1 km/h, they travelled constantly at such a rate for short distances only. The observed behaviour of Iriomote cats suggests that their generally slow movement rate may have resulted from frequent interruption of travel with short breaks for hunting and consuming prey. As the prey of Iriomote cats usually consists of small items, such as insects or small amphibians (Sakaguchi & Ono, 1994), the pauses may be undetectable by radio-telemetry.

Our study showed that the Iriomote cat moves relatively long daily distances at an unhurried rate, covering its home range with a dense net of winding routes. Few studies on other wild cat species present a detailed analysis of 24-h movements. The only studies of the leopard cat *Prionailurus bengalensis* (the nearest relative of the Iriomote cat) in Thailand by Rabinowitz (1990) and Grassman (2000) did not provide information on DMD. However, the daily movements reported there as straight line distances between consecutive daily locations (0.6–1.0 and 1.05 km, respectively) are similar to values obtained for Iriomote cats in this study.

groups of cats and seasons were calculated with Mann–Whitney *U*-test for pairwise comparisons. Significant differences were found in females with kittens only between seasons in days 2 and 3 ($U = 51, N_1 = 9, N_2 = 6, P < 0.01$ and: $U = 58, N_1 = 8, N_2 = 8, P < 0.005$, respectively).

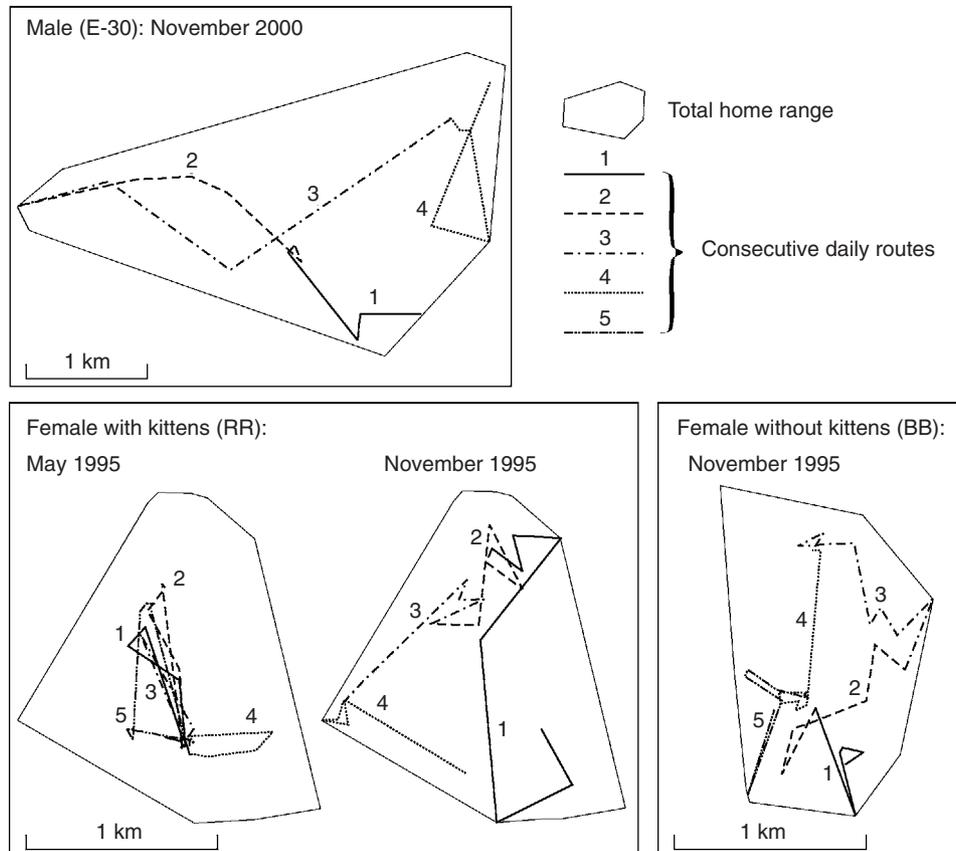


Fig. 4. Examples of daily movement routes by Iriomote cats *Prionailurus bengalensis iriomotensis* shown in their total home ranges. The movements of a female with kittens are shown for the nursing period (May) and for the period of the kittens' independence (November). The movement routes were based on continuous radio-tracking with locations taken every 3–4 h.

Despite a large variation in the home range and body sizes across various members of the *Felidae* family the DMD, SLD and speed are relatively similar (Table 5). While the home ranges may differ by three orders of magnitude, their movement distances and speed may differ by 2–6 times only, even between the largest and smallest species. Note that, as representatives of small felids, Iriomote cats moved daily distances of the same order as big cats. This supports the hypothesis concerning the constant movement rate in cats suggested by Jędrzejewski *et al.* (2002). On the other hand, movements of Iriomote cats should enable them to cover their small home ranges in greater detail than felids that have larger ranges. Indeed, a comparison of intensity of movement indices (IM) between the Iriomote cat and the Eurasian lynx revealed that the former species is using its range 95% more intensively than the latter. As a consequence, this should affect defensibility of the home ranges of Iriomote cats.

Given their small home ranges, it was presumed that Iriomote cats would show defensive behaviour in two ways: by visiting the entire area of their home ranges in a short period (for scent-marking), and by regular, rotational use of their ranges. Occasionally, cats were found crossing their entire ranges during a few days (see Fig. 4), which would indicate they are potentially able to patrol home ranges effectively (in terms of advertising their presence).

On the other hand, the routes of their daily movements covered an unexpectedly small portion of their total home ranges (up to 36% after 5 days), and the cats did not use home ranges in a rotational way. For comparison, the lynx used up to 15% of their much larger home areas in the same time (Jędrzejewski *et al.*, 2002). It suggests that, despite their ability to do so, Iriomote cats do not undertake efforts to actively defend their ranges. Unfortunately, it was not possible to test the consequences of such behaviour on the spatial relations among individuals directly, because individuals with adjacent ranges were not followed for long enough during the same period. Earlier studies of the Iriomote cats, however, reported either intrasexual exclusiveness of annual home ranges (Sakaguchi, 1994), or extensive overlap between males (Izawa & Doi, 1994). We propose that lack of apparent territorial activity in Iriomote cats could be related to the confinement of this population to a small island. Owing to complete isolation, transient individuals should occur in excess in the population. Large numbers of transients may lead to frequent encounters between resident and transient cats (both, direct or indirect by means of scent marking), which in effect may discourage resident individuals from showing strict territorial behaviour.

It has been commonly accepted that spacing pattern of males and females is greatly influenced by their different

Table 5. Comparison of movement (DMD, daily movement distance; SLD, straight-line distance and speed) and home-range characteristics in various species of Felidae

Species	DMD (km)		SLD (km)		Speed (km/h)		Home-range size (km ²)		Overlap%		Body weight (kg)	Source
	M	F	M	F	M	F	M	F	M	F	F–M	
<i>Lynx lynx</i>	–	–	5.9	2.0	–	–	1906	561	–	–	15–24	Sunde <i>et al.</i> , 2000
<i>Panthera tigris altaica</i>	9.6	7.0	–	–	–	–	1000	450	–	–	100–306	Yudakov & Nikolaev, 1979; Nowell & Jackson, 1996
<i>Puma concolor</i>	–	–	2.4	2.2	–	–	826	685	–	< 45	57	Hemker, Lindzey & Ackerman, 1984; Iriarte <i>et al.</i> , 1990
	6.4	–	4.6	3.1	0.8	–	767	218	6	25	30–60	Beier & Barret, 1993; Beier, Choate & Barrett, 1995; Dickson, 2001
	–	–	3.2	2.3	–	–	453	173–373	Little	High	50–75	Hornocker, 1970; Seidensticker <i>et al.</i> , 1973
<i>Panthera pardus</i>	12.2	8.4	–	–	–	–	451	188	46	43	25–45	Stander <i>et al.</i> , 1997
<i>Lynx lynx</i>	9.0	6.8	3.3	1.5	1.5	1.0	248	133	30	6	15–25	Schmidt <i>et al.</i> , 1997; Jędrzejewski <i>et al.</i> , 2002
<i>Panthera onca</i>	–	–	3.3	1.8	–	–	142	–	–	20–51	75–95	Crawshaw & Quigley, 1991
<i>Panthera pardus</i>	–	–	2.8	1.5	–	–	19–96	6–30	3–30	0–69	37–60	Bailey, 1993
	–	9.6	3.0	1.9	1.0	1.4	86	29	–	20	32–56	Jenny, 1996
	–	–	1–3	–	–	–	40–69	–	10–57	–	?	Norton & Henley, 1987
<i>Panthera tigris tigris</i>	2.7–9.6	–	2.8	2.2	0.7	–	60	17	0	0	116–230	Sunquist, 1981
<i>Panthera onca</i>	–	11	–	0.5–4	–	–	–	38	–	yes	60, 70	Schaller & Crawshaw, 1980
	–	–	–	–	0.8	–	33	–	High	–	57	Rabinowitz & Nottingham, 1986
<i>Lynx rufus</i>	–	–	2.1	1.4	–	–	26	15	5	3	8–9.5	Wassmer, Guenther & Layne, 1988
<i>Lynx pardinus</i>	8.7	6.4	–	–	–	–	25	20	15	20–30	9–16	Ferreras <i>et al.</i> , 1997
<i>Leopardus pardalis</i>	3.8	1.9	–	–	–	–	10.6	3.4	Excl.	Less excl.	8–10	Ludlow & Sunquist, 1987; Nowell & Jackson, 1996
	3.5–4.0	1.8–3.7	–	–	0.3 (max 1.4)	–	8.1	2.5	0	0	7–12	Emmons, 1988
<i>Prionailurus bengalensis</i>	–	–	0.6–1.0	0.8	–	–	7.5	6.6	0	–	2.5–3.5	Rabinowitz, 1990
	–	–	1.0–1.6	0.6	–	–	3.1–5.8	2.5	2.4	–	2.7–3.5	Grassman, 2000
<i>Prionailurus bengalensis iriomotensis</i>	3.2	2.2	1.0	0.6	0.3	0.2	2.8–5.8	1.4–4.0	High or little	High or little	3–4	This study; Izawa & Doi, 1994; Sakaguchi, 1994
<i>Felis silvestris</i>	5.8–8.2	5.2	–	–	0.8–1.1	0.5	5.7	1.8	Excl.	Excl.	2.8–6.0	Stahl, Artois & Aubert, 1988

reproductive tactics (as described by Sandell, 1989 for solitary predators). Sexual and seasonal differences in the movements characteristic of the Iriomote cats found in this study provide confirmation of this relationship. Male Iriomote cats seemed to be generally more mobile than females. They showed longer DMD, which is apparently related to patrolling their larger home ranges (Izawa *et al.*, 1991; Sakaguchi, 1994; this study). Moreover, the year-round stable SLD/DMD ratio in males suggests that they tended to maintain persistent control over the females included within their ranges. Their efficiency to do so could have additionally increased during the mating season, as they expanded their daily ranges (DMR), moved faster and more intensively (IM). Routes of females were presumably just as long as necessary for efficient foraging. Possibly, increased energetic demands (lactation and providing kittens with additional food) during nursing period drove breeding females to lower the SLD/DMD ratio (frequent returns to the den to nurse the kittens), and maintain equally long DMDs in both seasons. The nursing period (May–August) coincides with the season of greater availability of food on the island (Sakaguchi, 1994; Watanabe, 1999), which would allow the cats to shorten their daily distances to satisfy their energetic requirements. However, only non-reproducing females moved a shorter DMD at this time. The same reason probably caused them to use smaller DMRs, which would make them similar to females with kittens, but in contrast, they maintained a stable SLD and SLD/DMD ratio year-round.

Similar observations regarding sexual and seasonal variation in the movements of the Eurasian lynx were made by Jędrzejewski *et al.* (2002). However, unlike the lynx, the reproducing female Iriomote cats during September–April were moving in a similar manner to males, having covered long SLD in relation to DMD. Female lynx maintained their specific ‘concentrated’ long-distance movements with short SLDs during the entire year. This difference may result from the peculiar biology of the two species. Female lynxes stay with their kittens over winter (May–March), regularly providing them with food (Schmidt, 1998). In contrast, female Iriomote cats may remain solitary from August to April (Okamura *et al.*, 2000). Despite the mentioned similarity between male and female Iriomote cats, females moved their characteristic shorter DMD in both seasons.

Our study has contributed to the existing knowledge on the use of space in felids by providing a deeper insight on the movement pattern of the Iriomote cat and by showing its resemblance to other cats. However, owing to the possible effect of isolation of the population and the small size of the island on spacing by the cats, our results may be specific. Therefore, still more data are needed to understand fully the mechanisms determining the spatial organization of felid populations.

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APPENDIX. The Iriomote cats radio-tracked for study of movements pattern from 1993 to 2001

Cat's ID	Sex	Age	Time of monitoring	No. of locations	No. of locations in particular years	No. of full 24-h radio-tracking sessions	Home-range size (km ²)
RR ^a	F	Adult	6 Nov 1993–21 Oct 1996	540	54, 36, 355, 95	43	1.71; 1.96 ^c
BB ^a	F	Adult	6 Nov 1993–10 Nov 1995	236	69, 60, 107	13	1.44
SN ^a	M	Adult	30 Oct 1994–21 Oct 1996	160	17, 100, 43	7	4.57
W-46 ^a	F	Adult	26 Jun–5 Aug 1996	116	116	8	1.47
Nene ^b	F	Adult	12 Jun 2000–15 Feb 2001	617	457, 160	20	4.00
Yonku ^b	M	Adult	12 Jun 2000–8 Mar 2001	1186	525, 661	33	2.75
Omo ^b	M	Adult	12 Jun–29 Jul 2000	113	113	2	5.80
Oki ^b	M	Adult	16 Jun–24 Dec 2000	134	134	3	5.79
E-18 ^b	F	Adult	20 Sep–22 Oct 2000	286	286	7	2.35 ^d
E-36 ^b	F	Adult	18 Oct–22 Oct 2000	63	63	3	1.87 ^d
E-30 ^a	M	Adult	17 Nov 2000–20 Jan 2001	58	29, 29	8	5.77 ^d

^a Cats radio-tracked every 3–4 h.

^b Cats radio-tracked every 0.5–1 h.

^c Home range estimated for 2 yearly periods (1995 and 1996) before and after its spatial shift.

^d Home range estimated including data collected earlier by S. Watanabe (pers. obs.).