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Original article

Seasonal changes in the diet and diet selectivity of large Japanese moles, *Mogera wogura* (Temminck, 1842)

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Abstract

We investigated the foraging behavior of large Japanese moles (*Mogera wogura*). We collected several animals from a single site throughout the year and documented their stomach contents. We also collected soil samples throughout the year to measure the vertical distribution of potential prey items at the site. Oligochaeta and Coleopteran larvae were the greatest of potential prey items as the biomass in the soil and also the most numerous animals in the stomach contents. Based on the vertical distribution of soil animals, we assumed that the moles were foraging in the top 35 cm of soil. We evaluated prey selectivity by comparing the seasonal composition (by weight) of animals in the stomach with the seasonal composition (biomass) in the soil surface layers (0 to 35 cm). The moles tended to forage opportunistically, although Coleopteran larvae were selected preferentially and Isopoda were avoided. We also found seasonal changes in diet selectivity. Chilopoda were selected preferentially in winter. Therefore, we hypothesize that during winter when the soil biomass decreases, *M. wogura* capture prey by burrowing new tunnels although the moles forage on soil animals that fall into the tunnels during their patrols throughout the year.

Key words : Large Japanese mole, *Mogera wogura*, diet selectivity, stomach contents, soil animals

Introduction

Talpidae moles inhabit the subterranean ecotope throughout their entire life, feeding on animals that are also present in the soil (Godfrey and Crowcroft, 1960 ; Ondo and Fukuda, 1961 ; Abe, 1968 ; Mellanby, 1971 ; Funmilayo, 1979 ; Gorman and Stone, 1990 ; Hartman *et al.*, 2000 ; Beolchini and Loy, 2004). The moles construct and patrol tunnel systems to maintain their distinct home ranges, and also to forage the animals fall into the tunnels while new tunnels are occasionally dug to forage for animals that are in the soil (Godfrey and Crowcroft, 1960 ; Mellanby, 1971). At least two studies have shown that the stomach content of these moles is representative of the fauna present in the soil (Godfrey and Crowcroft, 1960 ; Funmilayo, 1979). Thus, moles are generally thought to be opportunistic foragers (Gorman and Stone, 1990). The seasonal changes that have been observed in their diet composition (Godfrey and Crowcroft, 1960 ; Funmilayo, 1979) are presumably due to changes in the vertical distribution of prey items in the soil (Gorman and Stone, 1990). Interestingly, there is some evidence that moles alter their vertical

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distribution to mirror that of the soil fauna that migrate deeper during winter or during droughts (Mellanby, 1971 ; Gorman and Stone, 1990). From ecological view point, "What do predators prey?" and "How are predators affected by others and the density of preys?," are subjects to study (Begon *et al.*, 1996). The moles that prey on the animals inhabiting soil vertically, have distinct foraging strategies from surface dwelling mammals. Unfortunately, because of their subterranean habitat little is known about the foraging strategies of moles.

The large Japanese mole (*Mogera wogura*) is distributed in the west part of Honshu Island and throughout Kyushu Island (Abe, 2005). These moles feed on animals that are present in the soil (Abe, 1968 ; Ondo and Fukuda, 1961). Ondo and Fukuda (1961) reported seasonal changes in the diet composition of *M. wogura*. However, the changes are likely biased due to differences in the site of collection (samples were collected from several sites such as rose garden and dune forestation area). There is some debate regarding the differences in stomach contents between populations from distinct habitats. The presence of differences is supported by Godfrey and Crowcroft (1960) but contradicted by Funmilayo (1979). In addition, the soil fauna differs according to the vegetation type of their habitat (Watanabe and Shidei, 1963). Given these factors, we conducted the current study at a single study site throughout the year.

Our objective was to elucidate seasonal changes in the diet of *M. wogura* and their foraging strategy. We captured moles at a single site throughout the year and enumerated the stomach contents. In addition, we collected soil samples to determine the vertical distribution of potential prey items. By comparing the stomach contents and the vertical distribution of soil animals, we estimated the foraging depth and resource selection of the moles.

Materials and Methods

Study site

The study was conducted in gardens of Japanese chestnuts (*Castanea crenata*) and Japanese persimmons (*Diospyros kaki*) which were adjoining and 0.9ha in area at the Field Science Center, University of Miyazaki, Miyazaki Prefecture, Kyushu, Japan. The understory vegetation consisted primarily of Italian rye grass (*Lolium multiflorum*).

Stomach content sampling

We collected 84 individual moles between May 2006 and April 2007. The moles were collected using tied up type or scissor type traps under the permission of the Miyazaki Prefecture. Following capture, the moles were immediately transported to the laboratory. The stomach was then dissected out and stored in 70% ethanol until the contents could be examined as follows. The excess ethanol was removed and the stomach contents were identified under a stereomicroscope. The animals were classified into the following categories : Oligochaeta (earthworms), Arachnida (spiders), Isopoda (pill bugs and sow bugs), Diplopoda (galleyworms), Chilopoda (centipedes), Orthoptera (mole crickets), Dermaptera (earwigs), Blattodea (termites), Hemiptera (cicada larvae and shield bugs), Coleopteran larvae and adults (beetles), Dipteran larvae (flies and gadflies), Lepidopteran larvae (cutworms), Hymenopteran larvae and adults (ants). The mass of each food item was determined using an electronic balance (0.001 g). We then calculated the percent frequency (percentage of moles that had consumed each food item) and percent weight (percentage contribution for each item to the total weight of food items) for each season. These were defined as spring (March to May), summer (June to August), autumn (September to November), and winter (December to February).

Prey item collection.

We set up three quadrates (50 × 50 cm) in each study site every month. Within each quadrate, we collected soil from 4 depths (0 − 5 cm, 5 − 35 cm, 35 − 65 cm, 65 − 95 cm deep). The soil was broken up and stored in a low-temperature room at 5℃. We then passed the soil through a 2 mm mesh sieve and collected the animals which remained on sieve and those that passed through the sieve. The animals were preserved in 70% ethanol solution until they could be examined. The animals were subsequently identified under a stereomicroscope and classified into the same categories as for the analysis of stomach contents. The mass of each category was determined using an electronic balance (0.001 g), and the wet weight was used to represent the biomass. The data were divided in the same four seasons as for the analysis of stomach contents. We examined the seasonal changes in the

total biomass and the biomass in each soil layer.

Statistical analysis and analysis of diet selectivity

We analyzed for seasonal changes in the total biomass of the soil animals in all layers, and between layers in each season using a Steel-Dwass test. We tested for dietary selectivity for each major prey category by comparing its contribution to the diet with its availability. The availability of each prey item i (a_i) was calculated by dividing the proportion of the biomass of prey items by the total biomass in each season. The utilization of each prey item i (u_i) was calculated by dividing the proportion of the wet weight of the prey items in the stomach by the total weight of the stomach contents in each season. We estimated the preference for prey items using a selection index (w_i), which was derived from $w_i = u_i/a_i$. A value of $w_i = 1$ indicated that there was no preference, a value > 1 indicates preference and a value < 1 indicates avoidance. Each w_i value was tested to calculate Bonferroni's confidence interval (Manly *et al.*, 2002).

Results

Seasonal changes in the stomach contents of large Japanese moles

The majority of the stomach contents (by weight) consisted of Oligochaeta (45.5 − 75.6%) and Coleopteran larvae (15.2 − 18.4%). However, the contribution of Hemiptera (5.0%) and Diptera (5.0%) increased in the summer. Similarly, the contribution of Chilopoda (10.1%) and Coleopteran adults (5.6%) increased in the winter. The contribution of all other categories of prey items was <5.0% (**Table 1**).

The frequency of occurrence differed somewhat from the results above. Coleopteran larvae (76.9 − 100.0%) were more numerous than Oligochaeta (66.7 − 87.5%). In addition, Chilopoda (54.2 − 76.5%), Coleopteran adults (40.0 − 61.5%), and Hymenopteran adults (29.2 − 50.0%) were also common. The number of Arachnida, Isopoda, Dermaptera, and Dipteran larvae was around 30% in all seasons. All other categories were present in <30% of the moles.

Table 1 Seasonal changes in the diet composition of the large Japanese mole *Mogera wogura*. Values represent the percent contribution to the total weight of stomach contents and parenthetic values represent the percentage of moles in which the prey item was found.

Food items (Order level)	Spring		Summer		Autumn		Winter	
Oligochaeta	64.6	(87.5)	64.3	(66.7)	75.6	(70.6)	45.5	(69.2)
Arachnida	0.3	(16.7)	0.5	(26.7)	0.2	(35.3)	0.0	(15.4)
Isopoda	0.7	(33.3)	0.2	(13.3)	0.2	(35.3)	0.7	(23.1)
Diplopoda	0.1	(12.5)	0.1	(10.0)	0.0	(5.9)	0.0	(7.7)
Chilopoda	2.5	(54.2)	1.4	(60.0)	3.2	(76.5)	10.1	(61.5)
Orthoptera	0.1	(4.2)	0.2	(6.7)	2.0	(52.9)	2.7	(15.4)
Dermaptera	1.0	(37.5)	0.8	(26.7)	0.7	(35.3)	1.3	(30.8)
Blattodea	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.1	(7.7)
Hemiptera	1.5	(25.0)	5.0	(16.7)	0.2	(23.5)	0.8	(7.7)
Coleoptera larvae	21.5	(100)	18.4	(100.0)	15.2	(94.1)	28.4	(76.9)
Coleoptera adults	3.1	(54.2)	3.7	(40.0)	1.0	(47.1)	5.6	(61.5)
Diptera	0.8	(37.5)	5.0	(33.3)	1.2	(5.9)	2.4	(30.8)
Lepidoptera	1.8	(20.8)	0.1	(3.3)	0.2	(11.8)	0.5	(15.4)
Hymenoptera larvae	0.7	(8.3)	0.0	(3.3)	0.0	(5.9)	0.1	(7.7)
Hymenoptera adults	1.3	(29.2)	0.3	(50.0)	0.2	(47.1)	1.8	(46.2)
N (Number of investigated moles)	24		30		17		13	

Seasonal changes in biomass and vertical distribution of the prey

The prey item biomass was highest in the autumn and lowest in the winter (**Fig. 1**). Most prey items were found in the surface (0−5 cm) layer, followed by the 5−35 cm layer, in all seasons (**Fig. 1**) The biomass in each layer did not change among the seasons (*Steel-Dwass test*, $P>0.05$). Oligochaeta (49.6−78.3%) and Isopoda (14.2−42.5%) contributed most to the biomass in the 0−5 cm layer, followed by Arachnida, Chilopoda, Dermaptera, Hemiptera, Coleopteran larvae and adults, Dipteran larvae, and Hymenopteran adults (<5% for each category) (**Table 2**). Similarly, Oligochaeta (5.2−37.3%), Coleopteran larvae (12.6−14.0%), Hymenopteran adults (9.2−22.1%) and larvae (10.8−14.6%) contributed most to the biomass in the 5−35 cm soil layer (**Table 2**). Coleopteran larvae and Hymenopteran adults and larvae were also found in the 35− 65 cm layer. Only Coleopteran and Hymenopteran larvae were found in the 65−95 cm layer (**Table 2**). Coleopteran larvae in the deeper layers tended to be smaller than in the shallower layers.

Relationship between foraging depth and diet selectivity in large Japanese moles

The majority of fauna constituting the prey of the large Japanese mole were found in the top two layers (0−5 cm and 5−35 cm). Therefore, we assume that the moles foraged in these layers. Based on a comparison of the ratio of prey items weights in the stomach and the ratio of the biomass of prey items in the soil, it appears that the majority of prey items were foraged opportunistically (**Table 3**). However, this analysis also suggested that Coleopteran larvae were preferred whereas Isopoda and others were avoided (**Table 3**). Chilopoda were selected preferentially in winter. Conversely Orthopteran and Lepidopteran larvae were avoided in the spring and summer, respectively (**Table 3**).

Discussion

Like other members of the Talpidae moles, large Japanese moles prey upon soil animals (Godfrey and Crowcroft, 1960 ; Ondo and Fukuda, 1961 ; Abe, 1968 ; Funmilayo, 1979 ; Gorman and Stone, 1990 ; Hartman *et al.*, 2000; Beolchini and Loy, 2004). The moles in the current study preyed most heavily on Oligochaeta and Coleopteran larvae. Other soil animals, such as Chilopoda and Hymenopteran adults were supplemental food items (**Table 1**). The moles tended to forage opportunistically in the shallower layers, although our data do suggest that they forage selectively on Coleopteran larvae and several subsets of the soil fauna (**Table 3**).
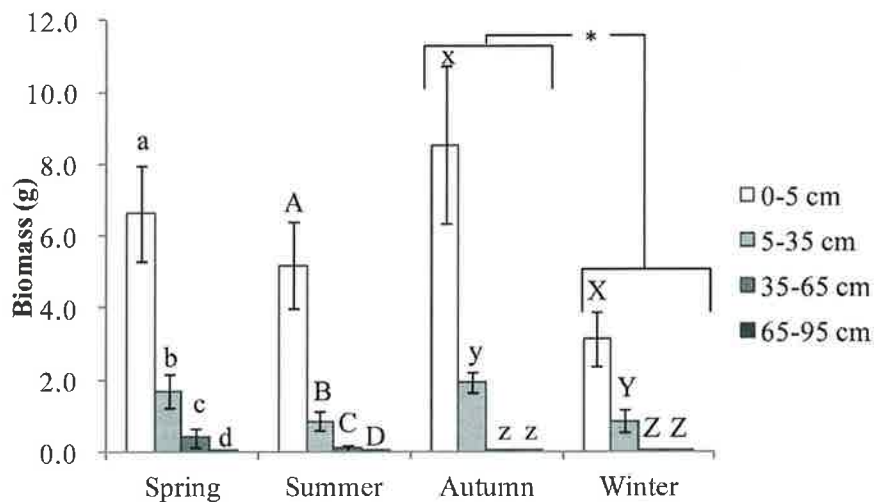

Fig. 1 The biomass of soil fauna that were collected in four subsurface soil layers during the four seasons. Subscripts that are different within each season represent significant differences in the total biomass among the layers (Spring ; a to d, Summer ; A to D, Autumn ; x to z, Winter ; X to Z, Steel-Dwass test, $P<0.05$). An asterisk denotes a significant difference in the total biomass between seasons (Steel-Dwass test, $P<0.05$)

Table 2 Seasonal changes in the biomass ratio of soil fauna in each soil layer

Food items (Order level)	0−5 cm				5−35 cm				35−65 cm				65−95 cm			
	SP	SU	AU	WI	SP	SU	AU	WI	SP	SU	AU	WI	SP	SU	AU	WI
Oligochaeta	63.6	78.3	61.3	49.6	5.2	21.1	37.3	34.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arachnida	1.8	1.1	0.8	3.4	0.2	0.3	0.0	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda	25.2	14.2	33.4	42.5	4.5	0.5	2.6	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diplopoda	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chilopoda	0.8	0.6	0.2	0.5	1.5	0.1	0.5	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orthoptera	1.1	0.0	0.0	0.0	34.6	0.5	10.9	15.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dermaptera	0.5	0.3	0.9	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Blattodea	0.1	0.0	0.0	0.5	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera	0.1	1.6	1.2	1.1	0.0	0.5	0.5	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera larvae	0.9	1.4	1.2	0.5	12.6	41.0	18.9	27.4	1.3	63.5	90.8	43.2	0.0	0.0	100.0	100.0
Coleoptera adults	2.5	1.7	0.7	0.3	2.8	0.0	11.1	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diptera	0.1	0.0	0.0	0.0	0.9	0.4	1.6	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepidoptera	0.0	0.0	0.0	0.0	1.1	9.1	1.2	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hymenoptera larvae	0.0	0.0	0.0	0.0	14.6	10.8	4.4	4.5	9.1	3.7	0.0	0.4	0.0	0.0	0.0	0.0
Hymenoptera adults	3.4	0.7	0.3	0.0	22.1	15.7	10.7	9.2	89.5	32.8	9.2	56.3	100.0	100.0	0.0	0.0

*Values are expressed as a percentage. Spring, summer, autumn and winter are abbreviated to SP, SU, AU, and WI, respectively.

Table 3 Diet selection by the large Japanese mole, *Mogera wogura* during each season

Food items (Order level)	Spring		Summer		Autumn		Spring	
	Wi	Bonferroni's CI	Wi	Bonferroni's CI	Wi	Bonferroni's CI	Wi	Bonferroni's CI
Oligochaeta	1.25	0.22	0.92	0.16	1.33	0.18	0.98	0.25
Isopoda	0.03	0.09	0.01	0.08	0.01	0.04	0.02	0.06
Chilopoda	2.64	3.89	2.57	5.11	11.36	14.68	11.83	8.31
Orthoptera	0.01	0.10	2.42	12.97	1.01	1.64	0.79	1.13
Dermaptera	2.65	6.28	3.01	7.88	1.00	2.72	1.14	2.31
Hemiptera	16.14	30.43	3.44	3.51	0.21	1.03	0.84	2.24
Coleoptera larvae	6.59	2.96	2.60	1.29	3.41	1.89	4.48	1.67
Coleoptera adults	1.21	1.59	2.49	2.99	0.37	0.88	7.14	6.91
Diptera	3.58	9.26	81.43	83.73	4.13	8.67	13.32	19.77
Lepidoptera	7.39	12.92	0.08	0.57	1.01	5.10	2.47	7.86
Hymenoptera adults	0.18	0.38	0.11	0.46	0.07	0.41	0.90	1.57
Others	0.25	0.55	0.22	0.68	0.12	0.66	0.06	0.28

In general, the prey items that were consumed by the large Japanese moles were consistent with other studies (Abe, 1968 ; Ondo and Fukuda, 1961). Ondo and Fukuda (1961) reported that the diet of large Japanese moles in Tottori Prefecture consisted primarily of (in order) Oligochaeta, Isopoda, and Hymenopteran adults and larvae. However, in our study, Hymenoptera and Isopoda were not primary food items. The Hymenoptera, although abundant, contributed less to the biomass than other soil animals (**Table 1**). Similarly, although Isopoda form a large part of the prey weight in the soil (**Table 2**), they were rarely consumed by the moles (**Table 1** and **3**).

The total biomass of potential prey items was higher in autumn and lower in winter. Furthermore, the biomass decreased gradually with depth (**Fig. 1**). We found no evidence for seasonal changes in the vertical distribution of Oligochaeta and Coleopteran larvae. Instead, smaller Coleopteran larvae and Hymenoptera tended to inhabit the deeper layers. Previously, seasonal changes in the diet composition of moles were reported to be correlated with changes in the vertical distribution of the soil fauna (Gorman and Stone, 1990). In these instances, it was described that the moles used the deeper layers to forage for the prey migrating deeper in the winter (Mellanby, 1971 ; Gorman and Stone, 1990). However, in our study, the soil animals were concentrated in the top 35 cm throughout the year. Therefore, we hypothesize that this population of large Japanese moles forage exclusively in the top 35 cm.

In general, the moles foraged opportunistically, however, Coleopteran larvae were selected preferentially throughout the year and Chilopoda were selected in winter. In contrast, the moles tended to avoid Isopoda throughout the year (**Table 3**). The seasonal changes in selectivity coincided with the onset of winter when the prey biomass decreased. Thus, we speculate that these other groups were consumed in lieu of the preferred prey items. The moles likely dig new tunnels to forage selectively on these groups. For example, we observed large numbers of Hymenopteran adults and larvae in a single stomach, suggesting the mole had recently excavated an ant nest. This is the evidence that moles may forage by digging the new tunnel for additional prey as well as by using their tunnel systems as a trap (Mellanby, 1971). We hypothesize that the moles did not consume Isopoda in the same ratio as they were present in the soil because of their nutritional value which is presumably poor or the depth at which they occur. It is unlikely that the moles encountered Isopoda with any regularity given they are only found near the surface. However, we have no direct evidence that either scenario explains the avoidance of Isopoda in the diet. In previous studies, the diet of other Talpidae moles tended to reflect the biomass composition of the soil fauna (Godfrey and Crowcroft, 1960; Fummilayo, 1979). In contrast, our data suggest that large Japanese moles prefer certain prey items. It is possible that our results were biased due to the continuous sampling at a single site.

In summary, the current study is the first to evaluate the diet of large Japanese moles at a single site throughout the year. Our results offer insights into the foraging behavior of these animals. Additional studies at other sites, and in different species will further our understanding of the diet and foraging behavior of moles. Furthermore, the relationship between diet selection and the nutritional value of the prey is of considerable interest as this information may explain the preferences for some prey items.

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コウベモグラ *Mogera wogura*（Temminck, 1842）の食餌構成と食物選択性の季節変化

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　コウベモグラ *Mogera wogura* の胃内容物を土壌動物の垂直分布とともに同一調査地点で継続的に調査し，これらの比較により採餌様式の解明を試みた．モグラは，土壌動物を主に採餌し，胃内容物では貧毛綱および鞘翅目幼虫の重量比あるいは出現頻度が高かった．モグラが餌として利用した土壌動物の生息深度から，モグラは年間を通して土壌深度0から 35 ㎝ までの部分で主として採餌すると推定した．この深度までの各土壌動物の現存量比と胃内容物中の重量比を季節ごとに比較すると．選択的に利用する鞘翅目幼虫や回避する等脚目を除きモグラは土壌動物を機会的に採餌するが，鞘翅目成虫のように季節によって選択的に利用するものも存在することが明らかになった．このことから，コウベモグラはトンネルシステムを巡回し，そこに落下した土壌動物を機会的に採餌し，土壌動物が減少する時季には、新たにトンネルを掘り土壌動物を捕食することが示唆された．

Original article

Subterranean spatial utilization of the lesser Japanese mole, *Mogera imaizumii* (Kuroda, 1957)

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Abstract

We investigated the subterranean spatial utilization of the lesser Japanese mole, *Mogera imaizumii*. We attached a radio transmitter to 8 individuals and conducted 9 sessions of continuous radio-tracking for up to 48 h. The depth of the moles was estimated based on the strength of the radio signal. In addition, we measured soil temperature and the abundance of soil animals as potential prey items at several depths to determine their effect on the vertical distribution of the moles. The home range size was negatively correlated with the total biomass of soil animals and the home range was expanded during the breeding season. The vertical distribution of the moles changed seasonally. A soil temperature of 23.0℃ appeared to be the threshold above which the moles chose to use the shallow soil layers. The utilization of this zone during the winter was likely due to the overlap with the breeding season. During this period, male moles actively search for receptive females. In summary, our data suggest that the seasonal changes in the vertical distribution of moles may be explained, in part, by changes in soil temperature. Furthermore, reproductive state may also play a role in determining the vertical distribution of individual moles.

Key words : Lesser Japanese mole, *Mogera imaizumii*, depth utilization, home range, radio telemetry.

Introduction

A number of subterranean mammal species construct tunnel systems in which they spend the majority of their life. These tunnels provide a stable microclimate and shelter from terrestrial predators (Nevo, 1999 ; Buffenstein, 2000 ; Busch *et al.*, 2000 ; Burda *et al.*, 2007). The tunnel systems typically consist of shallow and deep tunnels that extend both horizontally and vertically underground. It is generally thought that the shallow tunnels are used for foraging whereas the deeper tunnels are thought to provide refuge from predators and a more favorable microclimate (Nevo, 1999 ; Burda *et al.*, 2007). However, little is known about the use of these tunnel systems because of the difficulties observing the behavior of subterranean mammals.

Moles are known to construct elaborate, three dimensional tunnel systems (Godfrey and Crowcroft, 1960 ; Mellanby, 1971 ; Hartman, 1983 ; Gorman and Stone, 1990 ; Yokohata, 1998 ; Yoshiyuki, 2002). These animals spend their entire life in these tunnels where they forage, breed, and rear their young. During the summer the moles create shallow tunnels that are

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visible from the surface. Conversely, in the winter, the presence of mole-hills signifies that the moles are removing soil from deeper tunnels. Based on these observations, it is thought that the vertical distribution of moles varies seasonally (Godfrey and Crowcroft, 1960 ; Mellanby, 1971 ; Gorman and Stone, 1990). It is hypothesized that the seasonal changes in vertical distribution is a response to changes in soil temperature and/or distribution of their prey (Godfrey and Crowcroft, 1960 ; Mellanby, 1971 ; Gorman and Stone, 1990).

The fully fossorial lifestyle of the moles prevents biologists from observing their behavior. However, the development of radio telemetry systems has allowed researchers to study home range distribution, seasonal changes in home range utilization, and the relationship between home range size and habitat quality (Stone and Gorman, 1985 ; Gorman and Stone, 1990 ; Loy et al., 1992, 1994 ; Beolchini et al., 1996). For example, a number of studies have shown that the home range of the male European mole, Talpa europaea, does not overlap with other males, but does overlap with the home ranges of several females. Furthermore, female home ranges often overlap those of other females (Stone and Gorman, 1985 ; Gorman and Stone, 1990). Gorman and Stone (1990) also showed that there was a negative relationship between food density and territory size in the European mole. Interestingly, both the pattern of home range overlap among individuals and the relationship between food density and home range size is similar in the Roman mole, T. romana (Loy et al., 1992, 1994 ; Beolchini et al., 1996). Loy et al. (1994) also observed patrolling behavior during the active period and seasonal changes in home range utilization in the Roman mole.

These studies highlight the utility of radio telemetry for evaluating the behavior of subterranean mammals. However, few studies have evaluated seasonal changes in depth utilization in moles. Our objective was to evaluate the seasonal changes in vertical distribution of the lesser Japanese mole, M. imaizumii. This species is endemic to Japan and is found primarily in the east area of Honshu, Japan (Abe, 2005). We radio tagged several individuals during a two year period and monitored their movement for up to two days. In addition, we measured soil temperature and soil animal biomass at several depths to determine the relationship between vertical distribution of the moles and soil temperature or prey abundance.

Methods

Study area

The study was conducted in the gardens of the Atsugi Campus, Tokyo University of Agriculture, Kanagawa Prefecture between May 2004 and February 2006. The garden had a number of trees, including Japanese zelkova Zelkova serrata, camellia Camellia japonica, Japanese cherry Prunus x yedoensis, and Japanese plum P. mume. In addition, the garden contained several ground cover plants from the Poaceae family (bristle grass Setaria viridis, zoysia Zoysia japonica, and silver grasses Miscanthus spp.) and the forb guild (fleawort Plantago asiatica, dandelion Taraxacum officinale, Japanese dock Rumex obtusifolius, shepherd's purse Capsella bursa-pastoris, and Cockleburs Xathium spp.). These latter plants were mowed 2-3 times/year using a bush cutter.

Determination of depth use by the moles

Prior to the study, we evaluated the relationship between transmitter signal strength and the depth of the transmitter below ground. The transmitters (50 MHz, Applied Biology, Co. Ltd., Japan ; 144 MHz, Arcitech Co. Ltd., Japan) were buried at depths of 5, 30, 50, 100, and 150 cm. The radio signal was recorded using a receiver (FT-817, Vertex Standard Co., Ltd., Japan) that was connected to a Yagi antenna (HY-144, Natec Co., Ltd., Japan). The antenna was held vertical to the ground and parallel to the body of the operator. We recorded the signal strength (S value) of the radio signal emitted from the tags at each depth. We then used the S values to determine subterranean depth of the moles during the study.

Mole trapping and attachment of the transmitter

We set mole live traps (Konishi type, Konishi Factory Co., Ltd., Japan) in the center of the opening to each tunnel. The traps were checked at intervals of 3 − 4 h and any moles that were captured were transported to the laboratory for tagging. We recorded the weight and sex (where possible). We evaluated the reproductive state by checking for the presence of an external generative organ in the males. Each mole was then anesthetized using a combination of ether gas and an injection of pentobarbital (Nembutal, Dainippon Sumitomo Pharma Co., Ltd., Japan) or ketamine (Ketalar, Daiichi Sankyo Co., Ltd., Japan).

Once the animal was fully anesthetized, we inserted a microchip (BioMedic Data Systems Inc., U. S. A.) under the skin on the back of the mole for individual identification. A radio transmitter was then glued to the dorsal surface at the base of the tail and secured with surgical silk. The area of attachment was shaved to ensure the transmitter adhered to the body. The animal was then allowed to recover from anesthesia and was released at the point of capture.

Radio telemetry

We recorded the highest *S value* reading every 5 min and marked the location using a numbered wooden peg. During the observations, we attempted to hold the antenna in the same manner as during the initial calibration. Each animal was monitored for up to 48 h continuously, or until the transmitter was shed. We tagged a total of 8 individuals and were able to determine the sex of 4 individuals (**Table 1**). Individual "C" was captured and tagged in both June and August, 2004. The sex of individuals "C" and "D" was determined by autopsy when recaptured. Individual "H" was classified as a male based on the presence of a penis. The mole's behavior was divided into two categories, active and inactive, based on their locomotor activity. The mole's behavior was classified as active when they were moving or when the *S values* were unstable. Conversely, their behavior was classified as inactive if the mole was stationary or the *S value* was stable for > 15 min.

The home range size of each mole was estimated using a 100% minimum convex polygon. The areas of the study site that were inaccessible to the moles (e.g. buildings) were removed from the calculation of home range size. The distance traveled by each mole was estimated by summing the linear distance between consecutive records (5 min apart).

Soil temperature and vertical distribution of soil animals

We monitored soil temperature every h at depths of 5, 30, 50, and 100 cm using thermal data loggers (RTR-51, T&D Co., Japan; TL-TH1, Taisei E&L Co., Japan). We used the hourly soil temperature data that was collected during the period overlapping the radio tracking to represent the thermal data for the month. The thermal logger failed in February 2006, therefore, the data from February 2005 were used to represent this period. We evaluated the subterranean vertical distribution of the soil animals between April 2005 and February 2006. We established 3 quadrates (50 × 50 cm) in the study area and collected soil from several layers (0-5, 5-35, 35-65, and 65-95 cm) within each quadrate. The samples were sifted using a 2 mm mesh sieve and any animals were removed by hand and stored in a 70% ethanol solution. The animals were classified to

Table 1 Sex, body size, behavior, and home range size of the moles tracked in the current study. Values in parenthesis of the study period represent the total hours tracked for each mole.

Mole	Sex[1]	Body mass[2] (g)	Study period- Month and year	Home-range size (m²)	Duration of the active period (min)	Distance traveled[3] (m/5 min)
A	—	64.7	Apr., '04 (41)	1502	138.1 ± 20.0	—
B	—	—	May, '04 (51.7)	916	170.6 ± 35.6	—
C	♀	67.0	Jun., '04 (49.7)	205	123.8 ± 17.3	—
C	♀	74.0	Aug., '04 (33.9)	113	146.9 ± 24.2	—
D	♂	85.6	Jun., '05 (18)	234	341.7 ± 121.3	2.2 ± 0.7
E	—	70.0	Aug., '05 (11)	382	108.3 ± 17.4	2.7 ± 0.3
F	—	78.4	Sep., '05 (26.5)	107	173.3 ± 39.9	0.7 ± 0.2
G	—	84.0	Oct., '05 (22.1)	1818	247.0 ± 40.4	4.1 ± 0.9
H	♂	85.1	Feb., '06 (33.9)	8165	106.9 ± 22.9	3.2 ± 1.1

[1] — : gender undetermined by appearance of individual.
[2] Individual B was not weighed.
[3] The distance traveled was not measured in individuals A – C.

the levels of class and order and then weighed to calculate the biomass at 5, 30, 60, and 100 cm depth, respectively.

Statistical analyses for the factors on depth utilization

We used a Chi-square test to evaluate the relationships between month and the rate of depth utilization during the active and inactive periods. The effects of season and soil depth on soil animal biomass and soil temperature, and the effect of study period on distance traveled were analyzed using a Wilcoxon test. We used the Spearman rank correlation test to evaluate the factors affecting home range size. The effects of soil temperature gradient or the vertical distribution of soil animals on the moles' use of the surface layer was analyzed using a logistic regression model. The binary "response" variable was calculated as the count of all observations where the moles were ≤5 cm or >5 cm below the surface. The explanatory variables included soil temperature gradient and the vertical distribution of soil animals. The soil temperature gradient, measured from the surface, was categorized as "high to low" or "low to high" by comparison of the mean soil temperatures among depths during each study period. The vertical distribution of soil animals was categorized as "superior to poor" and "poor to superior" based on a comparison of biomass among the soil layers during each study period. We used a logistic regression model to evaluate the relationship between the vertical distribution of the moles and soil temperatures and soil animal biomass. We pooled the data for the same month between years, regardless of any differences. The response variable was assigned a value of 1 if a depth was "used" and 0 if the depth was "unused". The explanatory variables included soil temperature (four categories "a" to "d" based on a comparison of the hourly temperatures from each depth) and soil animal biomass (four categories "A" to "D" based on a comparison of the biomass from each soil layer). These explanatory variables were analyzed separately. To include soil temperature in the analysis, we calculated three dummy variables, "X_a", "X_b", and "X_c", as follows: if a given category was selected during a 5 min period, the selected category parameter was assigned a value of "1" and all others were assigned a value of "0". The lowest temperature category in each month ("d") represented the reference category, and the parameters associated with $X_a - X_c$ provide a comparison of each category with category d. To include the biomass of animals in the analysis, we included three dummy variables, "X_A", "X_B", and "X_C". These were calculated using the following method : if a given category of soil animal biomass was selected during a five min period, the selected category parameter was assigned a value of "1" and all other categories were assigned a value of "0". The lowest biomass value in each month, category "D", represented the reference category. The parameters associated with $X_A - X_C$ provide a comparison of each category with category D.

All analyses were conducted in JMP 5.1.1 (SAS Institute Japan Ltd., Japan)

Results

Home range, distance traveled, and activity pattern

The mean body mass and the home range size were 75.9 ± 2.71 (mean ± SE) g and 1389 ± 776 m² respectively (**Table 1**). There was no significant correlation between body mass and the home range size ($p = -0.0500$, $P > 0.05$). The moles had 3 − 4 distinct periods where they were active or inactive during a single day. The duration of the active period was variable both among and within individuals. The distance traveled per 5 min period was significantly different among the months ($P < 0.01$). In contrast, there was no correlation between the distance traveled and home range size ($p = -0.2105$, $P > 0.05$).

Seasonal changes in the subterranean depth utilization

The subterranean depth utilization during the active and inactive periods varied significantly among the seasons (active period : $\chi^2 = 1438.032$, $P < 0.01$; inactive period : $\chi^2 = 695.037$, $P < 0.01$; **Table 2**).

Seasonal changes in the soil temperature

Soil temperature varied significantly ($P < 0.001$) with depth (**Table 3**). We also observed significant monthly variation in soil temperatures in each layer ($P < 0.001$). The thermal gradient during spring was reversed during the winter.

Subterranean vertical distribution of soil animals

We collected the following animals in the soil samples : Oligochaeta (earthworms), Arachnida (spiders), Amphipoda (sand hoppers), Diplopoda (galleyworms), Chilopoda (centipedes), Dermaptera