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Effect of Diet and Water Availability on *Rattus norvegicus* (Rodentia: Muridae) Distribution

Tatsuo Yabe

Abstract

The distribution of the Norway rat *Rattus norvegicus* extends from the subarctic to the subtropics in Japan; yet it is limited by several factors. I discuss appropriate diet, water balance, and temperature as limiting factors based on surveys in the subarctic zone (Yururi-Moyururi, uninhabited islands in Hokkaido), the temperate zone (a business district in Yokohama and an uninhabited islet, Kaiho-2 in Tokyo Bay), and the subtropics (the Hahajima Islands in the Ogasawara Archipelago) in Japan. In Yururi-Moyururi, the rats recruited new generations in their population not only in the summer but also under snow cover, probably by preying on carcasses of their own species. In Yokohama, peaks of recruitment of their new generations were found in the winter and the summer, though the season with peaks changed every year. In Kaiho-2, rats stopped recruiting in the winter because of dehydration, and over the winter the group lost body mass as a result of body fat consumption. In Hahajima, rats lost body mass and preyed mainly on plant matter because of chronic dehydration. I conclude that protein-rich diets and water balance, but not temperature, are basic factors in the distribution of the Norway rat.

Keywords: *Rattus norvegicus*, geographical distribution, limiting factor, protein-rich diet, water balance

1. Introduction

The Norway rat *Rattus norvegicus* Berkenhout is one of the commensal rodents, along with the roof rat *R. rattus* Linnaeus, the Polynesian rat *R. exulans* Peale, and the house mouse *Mus musculus* Linnaeus. These rodents expanded their distribution worldwide by taking advantage of human activities [1–3]. However, they have limitations in their geographical distributions. Brooks and Rowe [2] point out that Norway rats are fundamentally fitted to the temperate zone, and they are less prosperous in tropical and subtropical climate zones, whereas roof rats thrive in tropical and subtropical climate zones. The question arises as to whether Norway rats are fitted to the temperate zone due to the mild temperature. Tomich [4] points out that mild temperature is secondary to appropriate diet as a factor in determining the Norway rat distribution. Although they are omnivorous, Norway rats require a diet containing a certain amount of animal matter or that is protein-rich [5–7].

Many species of seabirds nesting on or near the ground or in burrows are vulnerable to predation by Norway rats because of the terrestrial behavior of the rats [1, 8]. Rats on an island in the Aleutians were supposed to prey on seabirds and

to restrict the productivity of shorebirds and land birds by preying on the birds' food [9]. For Norway rats, such subarctic and subantarctic zones are severe environments in the cold season; when the rats' reproductive activities are depressed, their ears, legs, and tails are frostbitten, and their mortality rate is higher [10, 11]. However, Yabe et al. [12] discovered Norway rats breeding under snow cover on uninhabited subarctic islands in Japan. This fact suggests that they breed even during the cold season or under snow cover when an appropriate diet is available.

Also, the tropical and subtropical climate zones seem to be severe environments for Norway rats. Norway rats in the tropical climate zone are distributed in patches in limited areas such as seaports, irrigated villages, and large cities [2, 13–15]. Yabe et al. [7] found that the body mass of Norway rats on islands in the subtropical climate zone was smaller than those in the other habitats in the subarctic climate zone and the temperate climate zone in Japan because of a protein deficiency. Norway rats on the islands in the subtropical climate zone preferred plant matter to animal matter. On the other hand, Norway rats on an artificial islet in the temperate climate zone stopped breeding and lost body mass in the dry winter even though they preyed on some animal matter [16, 17]. Therefore, it seems that the appropriate diet changes depending on the habitat, and protein-rich diets do not always help Norway rats to thrive. Then commenting on the review by Yabe [18], I discuss the factors that cause the appropriate diet for Norway rats to shift based on their habitat and thus limit their geographical distributions.

2. Breeding in the subarctic zone

2.1 Breeding under snow cover

Yururi (168 ha, 43° 12' N, 145° 35' E) and Moyururi (31 ha, 43° 13' N, 145° 36' E) (referred to as Yururi-Moyururi hereafter) are uninhabited islands situated 2.5 and 3.7 km off the Nemuro Peninsula of Hokkaido, respectively (**Figure 1**). They are in the subarctic climate zone and have a mean annual temperature of 6.3°C. Both islands are flat and covered with low vegetation such as alpine plants and the bamboo grass *Sasa nipponica* Makino and Sibata. According to the local people, Norway rats intruded into these islands in the 1960s or 1970s from a boat used for fishing or light house construction.

Generally, the reproductive activities of Norway rats in the subarctic and subantarctic zones seem to be restricted in the summer. Schiller [11] found that the breeding season of Norway rats in a business district and in dumping sites in Nome in Alaska occurred exclusively in the summer. Pye and Bonner [10] also found that the breeding season of Norway rats in a coastal area on South Georgia Island in the subantarctic climate zone was in the summer from December to February. The most active breeding season for Norway rats on Yururi-Moyururi also seemed to be in the summer. Here, 63 (86.3%) of the 73 rats caught in late July and early August 2013 were born from June to July. However, 10 (13.7%) of them were born from December to March, the heavy snow season (**Table 1**) [12].

Data collected by a metrological station at Nemuro, a city close to these islands, show that the amounts of snowfall were 52, 41, 52, and 29 cm in December 2012 and January, February, and March 2013, respectively. No rats entered these islands in these years because boats are restricted from approaching these islands, and there were no wrecked vessels after these islands were appointed to be a sanctuary for birds in 2011. The distance from the Nemuro Peninsula to Yururi-Moyururi is over 1 km that is pointed out by Russell et al. [20] as a possible distance for Norway rats to swim. Therefore, the 10 rats on Yururi-Moyururi must have been born during

Figure 1.
Map of Yururi and Moyururi Islands, Yokohama, Kaiho-2, the Ogasawara Archipelago, and Hahajima Island [7].

the heavy snow season. Snow cover protects Norway rats from cold temperatures. The temperature at the ground level under 50 cm of snow cover, for example, is kept above -5°C , even when the air temperature is below -30°C [21]. Inukai [22] also showed that the temperature at the ground level under 1 m of snow cover was from 0 to -2.8°C when the air temperature ranged from -6 to -13°C in Sapporo, Hokkaido. Furthermore, deep snow cover stabilizes the temperature under the snow [23], and thus, snow cover likely provides comfortable breeding conditions for Norway rats. Maeda [24] also found evidence of the breeding of Norway rats under snow cover just after the melting of the snow in a forested area in Sapporo.

Age in months	Birth month	Number of rats			
		Male	Female	Total	Pregnant
1 (1.0–1.9)	July	28	24	52	7*
2 (2.0–2.9)s	June	10	1	11	1
3 (3.0–3.9)	May	0	0	0	0
4 (4.0–4.9)	April	0	0	0	0
5 (5.0–5.9)	March	3	0	3	0
6 (6.0–6.9)	February	1	3	4	2
7 (7.0–7.9)	January	0	2	2	1
8 (8.0–8.9)	December	1	0	1	0
Total		43	30	73	11

* 1.2–1.7 months old.
Seven females less than 2 months old were pregnant. Ages were estimated using a formula [12, 19] based on eye-lens weight. Birth month was calculated by subtracting the age from the date when the rat was caught. New data on pregnant females were added [12].

Table 1.
Age composition of Norway rats caught in late July to early August 2013 in Yururi-Moyururi.

2.2 Appropriate diet under snow cover

Norway rats on Yururi-Moyururi thrived and reproduced under snow cover without depending on human beings for their diet. In the case of Maeda [24], Norway rats ate mainly bamboo seeds and rodents such as gray red-backed voles *Myodes rufocanus* Sundevall, the population of which exploded after the bamboo-grass flowering. The voles usually make their nests in tunnels under ground, but in the snow season they make their nests and breed in the space under bamboo grass covered by snow [25, 26]. Therefore, it is likely that Norway rats could easily find and prey on such voles. However, there were no rodents or other small mammals except Norway rats on Yururi-Moyururi (T. Hashimoto, pers. comm.).

Birds of prey such as common buzzards *Buteo Buteo japonicus* Temminck and Schlegel are known to live on Yururi-Moyururi [27, 28]. It is likely that shallow snow and dead grass cover these islands at the end of autumn or beginning of winter. Rats running across such white snow are vulnerable to birds of prey [29], and rats running on dead grass may also be. Among birds of prey, common buzzards are known to feed on Norway rats [30], and they probably leave behind body parts of the prey as in the case of roof rats (Figure 2). The dense population of rats that were born during the summer will provide the necrophagous rats with many rat remnants as a food supply to winter and breed under snow cover. All the rats in Yururi-Moyururi were less than 9 months old (Table 2). This suggests that their life spans were shorter than in any other habitats such as the Hahajima Islands, a business district in Yokohama and an islet (Kaiho-2) in Tokyo Bay. Norway rats that were 13 months old or older were common in the latter three habitats (Table 2). Predation by birds of prey was probably one of the causes of their short life span. Snow cover in the heavy snow season protected Norway rats from such predators and helped them to breed during the winter.

2.3 Appropriate diets for breeding in summer

Meehan [31] reported that Norway rats become sexually mature at 2–3 months old, but it has also been found that they can become mature at less than 2 months old

Figure 2.
*Remains of roof rats *Rattus rattus* left by common buzzards *Buteo buteo japonicus* in the Ogasawara Archipelago (A: by T. Yabe; B: by F. Nomura, provided by PREC Inst. Inc.).*

Locality	Age in months		Total	% of ≥ 13	Reference
	<13	≥ 13			
Hahajima Islands	32	42	74	56.8	[7]
Yururi-Moyururi	73	0	73	0.0	[7, 12]
Yokohama	97	20	117	17.1	[7, 45]
Kaiho-2	210	5	215	2.3	[16]

The numbers of both sexes were combined. All the rats in Yururi-Moyururi were less than 9 months old. See Table 1.

Table 2.
Percentage of the number of Norway rats that were 13 months old or more in Hahajima Islands, Yururi-Moyururi, Yokohama and Kaiho-2.

[32–34]. On Yururi-Moyururi, seven young rats less than 2 months old were pregnant in the summer (Table 1). Why did Norway rats on Yururi-Moyururi tend to mature at a young age and breed actively in the summer? It is possible that a protein-rich diet

helped the rats to mature at a young age, as suggested by McCoy [5], who pointed out that a high-protein diet produces excellent reproductive conditions. Animal matter occupied $72.4 \pm 39.8\%$ ($n = 38$) by volume of the stomach contents of the rats in July–August 2013 in Yururi-Moyururi, and of this $11.9 \pm 30.1\%$ of rhinoceros auklets *Cerorhinca monocerata* Pallas [12]. From May to August, seabirds such as *Fratercula cirrhata* Pallas, *Cephus carbo* Pallas, *Uria aalge* Pontoppidan, *Larus crassirostris* Vieillot, *Phalacrocorax urile* Gmelin, *P. capillatus* Temminck and Schlegel, and *P. pelagicus* Pallas also stay on Yururi-Moyururi to breed [35]. Norway rats probably prey on adults, nestlings, and eggs of these seabirds, which would supply the rats with sufficient nutrition to mature at a young age and engage in active breeding. Therefore, it is likely that Norway rats on Yururi-Moyururi depend on a diet of seabirds for their reproductive activities in the summer and a diet of carcasses of their own species under snow cover in the winter.

Norway rats preyed on adult *C. monocerata* irrespective of the body weight of the rats. The mean body weight of the predators, 187.7 ± 75.8 g ($n = 16$), was not significantly different ($P = 0.09$) from that of non-predators, 147.2 ± 54.2 g ($n = 25$) [36]. On the other hand, only larger roof rats on the Chichijima Islands in the Ogasawara Archipelago preyed on Bulwer's petrels *Bulweria bulwerii* Jardine and Selby, where the mean body weight of the predators, 201.6 ± 27.5 g ($n = 22$), was significantly larger ($P = 3.0 \times 10^{-4}$) than that of non-predators, 167.5 ± 35.4 g ($n = 17$) [36, 37]. Norway rats preyed on adults of *C. monocerata* (520 g [38]) that were larger than themselves, whereas roof rats preyed on adults of *B. bulwerii* (78–130 g [39]) that were smaller than themselves. These findings show that Norway rats are more aggressive predators of animal matter than roof rats [36].

As for the water supply for the rats, peat bogs are a source of water in Yururi but there are no peat bogs in Moyururi. However, the area around the Nemuro Peninsula is covered by dense sea fog for 101.4 days a year, and over 16 days per month between June and August [40]. Therefore, dew from dense sea fog is probably one of the water sources for Norway rats. I hypothesize that a process was established by which Norway rats have an appropriate diet and engage in water supply for survival and a bimodal cycle of reproduction in the summer and under the snow cover on Yururi-Moyururi.

3. Breeding in temperate climate zone

3.1 Breeding independent of season

Davis [41] reported that generally, the pregnancy rate in Norway rats is low in cold and hot seasons, and as a result, the rate shows a bimodal curve, with the highest peaks in the spring and autumn. The breeding season is usually estimated from pregnancy rates in adult females (percentages of visible pregnancies). However, recruitments of new generations in the population are more essential than pregnancy rates in population analysis [41, 42]. We can estimate the trend in the fluctuations of reproductive activities or recruitments based on age compositions even using surveys conducted once a year. Moors [43] discussed the age composition based on the age index estimated from the upper molars in Norway rat populations in Noises Island in New Zealand and concluded that recruitments were more active in the summer than in the winter. However, this age index revealed indefinite ages. Pucek and Lowe [44] recommended the eye-lens weight as the best criterion among the known indices for determining the age of small mammals. Then, Yabe et al. [45] analyzed age compositions based on the eye-lens criterion in Norway rat populations in February or March 2014–2016 in a 21-ha business district in Yokohama in

the temperate climate zone (**Figure 1**). In this case, Norway rats showed recruitment peaks that were not always in the spring and autumn but also in the summer or winter, and the peaks changed every year (**Figure 3**). These results in Yokohama suggest that reproductive activities are controlled by factors other than temperature such as the food supply and environmental sanitation. In this business district in Yokohama, environmental sanitation activities conducted by volunteers control the Norway rat population [46].

3.2 Interruption of breeding by dehydration

Kaiho-2 (Fort No. 2) in Tokyo Bay (**Figure 1**; 4 ha, 35°18' N, 139°44' E) is an uninhabited islet in the temperate climate zone. This islet is covered with concrete, bricks, sand, sandy soil, grasses, herbs, and shrubs. Norway rats probably intruded into the islet in the early twentieth century, when a fort was constructed there. I discovered from the age compositions of the rats that their reproductive activities were interrupted around December or January [16, 17]. On average, between 1981 and 2010, in November, December, January, and February, the minimum temperatures were 9.6, 4.9, 2.3, and 2.6°C, and the amounts of precipitation were 107.0, 54.8, 58.9, and 67.5 mm, respectively, at Yokohama, a city close to Kaiho-2 [47]. Therefore, Kaiho-2 was dry in December and January compared with November and February. The water supply for Norway rats was probably insufficient around December and January because the amount of precipitation was low, the majority of succulent plants died, dew and standing water were limited, and the sandy soil lost moisture. Norway rats on the islet consumed protein-rich diets such as the mussel *Mytilus galloprovincialis* Lamarck and other marine invertebrates, which amounted to more than 50% of their stomach contents by volume, even in the winter [6]. However, such an invertebrate or protein-rich diet demands a large turnover of water [48]. Furthermore, most marine invertebrates including mussels are osmoconformers to the surrounding sea water [49]. Therefore, the interruption of reproductive activities during the winter was probably due to dehydration, but not to low temperature or food shortages.

Figure 3. Distributions of birth month and age in months in Norway rats caught in February or March 2014, 2015, and 2016 in Yokohama. Rats over 12 months old are excluded. Modified after [45].

Locality	Sex	Body weight (g)	
		3 Months	6 Months
Hahajima Islands	Male	77.0	112.6
	Female	79.5	102.9
Yururi-Moyururi	Male	208.3	278.5
	Female	156.3	205.1
Yokohama	Male	153.8	223.2
	Female	123.3	174.5
Kaiho-2 (non-wintered)	Male	193.3	281.3
	Female	168.9	259.9
Kaiho-2 (wintered)	Male	137.7	220.3
	Female	114.2	181.8

Pregnant females are excluded. Body weights were calculated from regression lines. See Figure 4.

Table 3.
Comparison of body weights of 3- and 6-month-old Norway rats living in the Hahajima Islands, Yururi-Moyururi, Yokohama, and Kaiho-2 (non-wintered and wintered groups) [7].

	Wintered [*]	Non-wintered [*]	Pregnant females
Kaiho-2	0.10 ± 0.04 ^a	0.16 ± 0.06 ^b	0.22 ± 0.06 ^c
n =	28	63	9
Shikine-jima	0.11 ± 0.06 ^a	0.12 ± 0.06 ^a	0.19 ± 0.07 ^c
n =	37	40	4

^{*}Excluding pregnant females.
Fat indexes were significantly different (t-test, *p* < 0.05) if they are followed by different letters. FI = 1.01FI^{*} + 0.01, where FI^{*} = fat free dry weight/dry weight [51].

Table 4.
Comparison of fat index (FI, mean ± SD) between wintered and non-wintered Norway rats on Kaiho-2 and a forested island (Shikine-jima) [17].

Collier and Levitsky [50] showed that albino *R. norvegicus* rats lose their body mass to maintain water balance when the water supply is insufficient. Moors [43] suggested that shortages of protein-rich diets and fresh water restrict the sexual maturity of females, litter sizes, and the growth of juveniles in Norway rats on Noises Island in New Zealand. It is likely that a similar situation occurred in Norway rats on Kaiho-2. The age composition of Norway rats on this islet showed a gap between the generations borne before and after the season around December and January, when breeding was interrupted. As a result, their population was divided into a wintered group and a non-wintered group based on the gap. The body mass of the wintered group was lower than that of the non-wintered group (Table 3). I compared a body fat index determined by the method of Yabe [51] among the wintered group, the non-wintered group, and pregnant females. Also, I compared the index between Kaih-2 and Shikine-jima (a 390-ha forested island in the Izu Archipelago, 34°19' N, 139°12' E) (Table 4). As a result, I found that the small body mass in the wintered group in Kaiho-2 was due to body fat loss [17]. The body fat indexes showed that pregnant females kept a high level of body fat irrespective of whether they were in the wintered or non-wintered group, or on Kaiho-2 or Shikine-jima. Pregnant females deposit body fat for reproduction, probably because they require more energy than nonreproducing females as was pointed out by Robbins [52]. The lost

body fat in the wintered group was not recovered after the dehydration period, and the non-wintered group kept a high level of body fat [16, 17]. This fat deposition procedure is different from that in mammals, which deposit body fat as a prelude to times when the energy intake will be less than the energy expenditure [52].

4. Dehydration and low body mass in subtropics

The Ogasawara Archipelago (Bonin Islands, Ogasawara Islands) is composed of the Mukojima Islands, the Chichijima Islands, the Hahajima Islands, and the Kazan (Volcano) Islands in the subtropics (**Figure 1**). Norway rats are thought to have intruded into the Ogasawara Archipelago between 1660 and 1862, but now they are living only in the Hahajima Islands and the Kazan Islands [53–55]. On the other hand, roof rats are prosperous and are distributed in most islands in the archipelago [56, 57], although they intruded there in the 1910s or 1920s, later than the Norway rats [54, 58]. It remains to be clarified why Norway rats are restricted to only a few islands in the archipelago.

The body mass of Norway rats on the Hahajima Islands is about half the weight of Norway rats on Yururi-Moyururi, Yokohama, and Kaiho-2 (**Table 3** and **Figure 4**). The low mass of the Hahajima rats was due to environmental factors rather than genetic factors such as Bergman's rule and the founder's effect. This was proved by the fact that the head and body length, tail length, and length of the upper molar row were not significantly different between the rats from Hahajima and those from other localities [7]. Therefore, the skeletons were the same but the body masses were different between the Hahajima rats and the others.

Norway rats on the Hahajima Islands tended to feed on plant matter such as fruits and seeds ($95.2 \pm 21.8\%$, $n = 21$, by volume percentage in stomach contents) and no seashore animals were found even in rats living close to the seashore [7]. This is an abnormal food habit in the Norway rat, which prefers animal matter [6]. As I previously mentioned, preying on plant matter helps maintain water balance because the consumption of animal matter or of a protein-rich diet requires more water intake. However, this change in food habits may lead to a protein deficiency and body weight loss in the rats. To meet their energy requirements, mammals consume their gastrointestinal contents first, but finally they utilize their body fat and protein, which leads to long-term weight loss [52]. Moors [43] suggests that a shortage of protein-rich diets and fresh water limited the reproductive activities of Norway rats on Noises Island in New Zealand. It is likely that on the Hahajima Islands as well, protein deficiency and dehydration decrease the weight and inactivated the reproduction of Norway rats. I suppose that Norway rats on the Hahajima Islands are less aggressive predators than rats living in the other habitats because of their food habit.

The Ogasawara Archipelago is probably an uncomfortable habitat for Norway rats due to chronic dehydration, which restricts their distribution. In the Hahajima Islands, there are streams and ponds on the main island but not on the surrounding islands. However, Norway rats were found even on the surrounding islands and in areas far from such water sources [7]. Therefore, dehydration in Norway rats on the Hahajima Islands was not due to a lack of such water sources. The mean annual precipitation in the Chichijima Islands from 1971 to 2000 was 1280 mm, and the mean potential evaporation (the amount of evaporation that would occur when enough water is given) was 1380 mm [27]. The former is less than the latter, and as a result, the soil tends to be dry. This indicates a potential cause of dehydration in Norway rats. However, the Hahajima Islands, with a mountain 462 m in height, is foggy and more humid than the Chichijima Islands, with a mountain 326 m in height, and the

Figure 4.

Comparison of body weight in grams (Y) and log value of age in months (X) and resulting regression lines for male and female Norway rats from the Hahajima Islands, Yururi-Moyururi, and a business district in Yokohama excluding pregnant females, showing infection with rat lungworms (*Angiostrongylus cantonensis*) [7]. Circles and triangles show rats that were negative and those that were positive for the infection, respectively.

low and flat Mukojima Islands [27]. Therefore, Norway rats probably thrive better in the Hahajima Islands than in the others.

Renal structures show that the ability to concentrate urinary water in Norway rats is like that in roof rats [59]. However, protein-rich diets demand a larger turnover of water than diets rich in carbohydrates or fat [48], and Norway rats feed on protein-rich diets, whereas roof rats prefer plant matter to animal matter [6]. Therefore, Norway rats require more water intake than roof rats. This difference in water requirements is probably one of the factors that separate the two species in the geographical distribution especially in tropical and subtropical climate zones [15]. Mild temperature is a secondary factor in determining the Norway rat distribution, after water balance and an appropriate diet. Even in the tropical climate zone, Norway rats are prosperous in large cities such as Bangkok (13° 44' N, 100° 29' E) and Chanthaburi (12° 36' N, 102° 06' E) in Thailand, which are surrounded by networks of watercourses and damp environments [15, 60]. Generally, in these habitats, there are protein-rich diets including garbage and invertebrates such as earthworms and insects [6]. Therefore, protein-rich diets and the means for avoiding dehydration such as creeks and sewage provide Norway rats with thriving habitats in large cities. These facts suggest that diets rich in animal matter or protein are associated with water balance, which are essential factors in the geographical distribution of Norway rats.

5. Conclusion

Mild temperature is a secondary factor in the reproductive activities of Norway rats as was proved by the results in Yururi-Moyururi in the subarctic zone and

in an urban area in Yokohama in the temperate zone. In Yururi-Moyururi, the rats recruited new generations in their population under snow cover probably by preying on remnants of their own species, which were left by birds of prey such as common buzzards. In Yokohama, the rats showed peaks of recruitment even in the summer and winter, though the season of the peaks changed every year. Even in the tropics, the rats are prosperous in large cities such as Bangkok and Chanthaburi in Thailand, which are surrounded by networks of watercourses and damp environments [15, 60]. It is likely that watercourses supply the rats with an appropriate diet discarded from houses as well as with moist conditions.

Water balance and a protein-rich diet are essential factors in the reproductive activities and distribution of Norway rats as was shown by the results in Kaiho-2 and the Hahajima Islands. The rats on Kaiho-2 in the temperate zone stopped recruiting of new generations and lost body mass by consuming their body fat in the winter because of dehydration. In the Hahajima Islands in the subtropics, the rats fed mainly on plant matter to maintain water balance because of chronic dehydration, and as a result, they lost body mass. In this case, the rats probably avoided consuming animal matter or a protein-rich diet to maintain water balance, but they consumed protein from within their bodies instead. Norway rats usually feed on a protein-rich diet or animal matter, which differs from the food habits of roof rats, which prefer plant matter to animal matter (6). Thus, a protein-rich or animal matter diet is an appropriate diet for Norway rats.

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