Reproductive characteristics of the Yangtze vole (*Microtus fortis calamorum*) under laboratory feeding conditions

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ABSTRACT

The reproductive characteristics of a laboratory population of the vole *Microtus fortis calamorum* were examined. Voles were allowed to breed under laboratory feeding conditions. Over a period of 3 months, 61.82% of the 110 vole pairs examined produced 3 or 4 litters. There were 1–9 voles in each litter and the mean litter size was 4.67 ± 0.28 (mean $\pm$ SE). Most litters included 3–7 young voles, accounting for 83.62% of all litters. The mean farrowing interval was 25.9 days (range from 19 to 95 days), and the most farrowing intervals were 20–25 days, accounting for 79.9% of the total. When based on litter size, the reproductive index was 6.23, but was 3.42 when based on pup survival. The survival rate of offspring to weaning was 55.03%. The high rate of infanticide that occurred after removal of males from cages indicates that, in the laboratory, both parents need to be present prior to weaning.

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1. Introduction

The Yangtze vole (*Microtus fortis calamorum*, Thomas 1902), a small herbivore species (Rodentia, Cricetidae, Microtinae, *Microtus*), is widely distributed throughout the middle and lower reaches of Yangtze valley. In the Dongting Lake region, Hunan Province, China, this subspecies of *M. fortis* is an agricultural pest and serves as a reservoir for human pathogens (Chen et al., 1998; Zhang et al., 2007, 2014). The Dongting Lake region is located in the middle of the Yangtze Valley in the northern part of Hunan Province, China (111°40′–113°10′ E and 28°30′–30°20′ N). During the dry season, the vole primarily lives on the beaches of Dongting Lake (October–June). During the wet season (June–October), the beaches flood and the voles migrate to the surrounding cropland (Guo et al., 1997). In some years, the population of migrant voles is large enough to cause serious damage to crops (Chen et al., 1998). For example, in 2007, a vole outbreak inflicted serious crop damage and attracted wide media attention (Zhang et al., 2007).

On the other hand, the Yangtze vole is the only known mammal species with natural resistance to schistosomiasis. There are many reports of the immunological characteristics of *M. fortis calamorum*'s innate resistance to *Schistosoma japonicum* infection (Zhu et al., 1991; He et al., 1999a,b; Li et al., 2001). As part of the search for anti-schictosomiasis substances, some researchers have been investigating the mechanisms underlying the anti-schistosome effects observed in *M. fortis* and the molecules involved in their natural resistance to *S. japonicum* infection (Liu et al., 2001; Jia et al., 2008; Jiang et al., 2008; Sun et al., 2008; Song et al., 2009; Gong et al., 2010; Hu et al., 2010, 2012; Wang et al., 2010; Cheng et al., 2011; Xiang

et al., 2012). *M. fortis* could also be developed as an experimental animal model of diabetes mellitus and spontaneous ovarian cancer that can be used in a variety of research, such as examination of pathological changes, pathogenesis, drug treatment, and vaccine development (Xiao and Wang, 2008). In order to both control pests in the wild and to develop a vaccine against schistosomiasis based on the natural resistance of Yangtze voles to the disease, it is necessary to breed the vole in the laboratory.

To establish a laboratory population, more than 100 voles were captured from Dongting Lake beaches in 2009. After 3 years of breeding in the laboratory, the population has become a stable breeding population that can reproduce throughout the year and successfully reach reproductive age under the artificial feeding conditions in the laboratory.

Laboratory observations on the growth and development of juvenile Yangtze voles have been performed (Wu, 1996). Ear erection occurs when pups are 3 days old and sex can be distinguished at the age of 4 days. Hair cover is complete at 8 days of age. Eyes open approximately 8–10 days after birth. All teeth emerge at approximately 10 days of age. Young are altricial and juveniles can live independently at 15–20 days of age. Pups mature within approximately 50 days to 2 months after birth. Body weight data can be fitted with a logistic curve. Our observations resembled the relevant available values. However, there have been no detailed reports regarding the reproductive characteristics of the vole after establishment of a breeding population. Here, we report basic information about Yangtze vole breeding characteristics in an established laboratory population.

2. Materials and methods

2.1. Animals and housing conditions

The Yangtze voles used in this experiment originated from wild individuals captured in the Dongting Lake area in 2009, and were 11th or 12th generation descendants that were bred and maintained in the laboratory. For this experiment, we selected 110 pairs of voles that were about 3 months old, but that had not yet engaged in sexual activity. Three-month-old voles were used in the experiment to ensure that all individuals were adults. The environmental conditions of the animal house were partially controlled at a temperature of 20–22 °C and a 12L:12D light cycle. A 12L:12D light cycle was used to simulate the photoperiod experienced in the wild during the breeding season (Wu et al., 1996; Guo et al., 1999). Before pairing, individuals were housed in same-sex sibling groups to prevent inbreeding. Voles were reared in polypropylene cages (43 cm × 32 cm × 19 cm) with a stainless steel mesh lid, and were provided with coarse wood shavings. Food and water were provided ad libitum. The trials were carried out between April and August, 2012.

2.2. Experimental method

Breeding pairs (one male and one female) were housed separately in polypropylene cages (43 cm ×

32 cm × 19 cm). After pairing, the voles were observed from April to July 2012 under the same feeding and management conditions as for rearing. Pairs were usually checked daily to assess their well-being and to check parturition and litter sizes; the date of birth is referred to as day 0. Offspring were removed from the parents on the 20th day after birth or after the birth of a second litter, so that there was no more than one litter of pups in each cage at any time. Breeding date, farrowing interval (inter-litter interval, including the interval between pairing and birth of the first litter), litter size, mean litter size, pregnancy rate, offspring survival rate (the number of alive proportion of young that survived until weaning), and reproductive index were recorded and calculated. Three months after initial pairing, 30 breeding pairs of voles were dissected, and the number of embryos was recorded by counting viable embryos in the uteri of females. The males were removed from the cages of the remaining pairs and parturition date was recorded until no further births occurred.

2.3. Statistics and analysis

The following formulae were used to calculate breeding statistics:

Mean litter size = total number of pups/total litter number.

Pregnancy rate = total number of females reaching parturition/total number of females* 100%.

Index of reproduction = total number of pups in 3 months/all test voles.

Single sample K–S tests were used to analyze the normality of mean litter size and the number of survival days before weaning at different densities. For normally distributed data, means were compared using one-way analysis of variance (ANOVA) followed by an LSD post hoc test. Nonparametric Mann–Whitney U tests were used to compare groups of non-normally distributed data. Differences in the pregnancy rates of different parities were evaluated using chi-square tests. All statistical analyses were conducted using SPSS (V.16.0) software. Where appropriate, data are presented as means ± SE.

3. Results

3.1. Reproductive parameters

The reported reproductive parameters were based solely on data collected over 3 months because after that time, 30 pairs of voles were dissected and the remaining 80 pairs were separated. Among the 110 pairs of voles, 96 pairs bred successfully, and 61.82% of the pairs produced 3 or 4 litters over the 3-month observation period (Table 1). There were 1–9 young voles in each litter. In total, the females produced 293 litters and 1369 young voles. The average number of pups in each litter was 4.67 ± 0.10 and 83.62% of the litters included 3–7 pups (Table 2). The mean farrowing interval (including the interval between pairing and birth of the first litter) was 25.9 ± 0.6 days (range, 19–95 days; Table 3). Most farrowing intervals were 20–25 days, accounting for 79.9% of all intervals (Table 4). The reproductive index was 6.23 when based on litter size. The

Table 1

Reproductive parameters of *Microtus fortis calamorum* over a 3-month period in the laboratory. Values are means ± SE unless otherwise noted.

No. of parturitions per pair	No. of pairs	Rate in total pairs (%)	Litter size (range)	Sample size	Mean litter size[a]	No. offspring surviving to weaning	Weaning rate of offspring (%)
0	14	12.73	–	–	–	–	–
1	5	4.55	1–5	5	3.00 ± 2.00^a	1.80 ± 2.00	60.00
2	23	20.91	1–7	46	4.15 ± 0.69^a	1.96 ± 0.69	47.23
3	30	27.27	1–9	90	4.38 ± 0.50^a	2.48 ± 0.50	56.62
4	38	34.55	1–9	152	5.06 ± 0.39^b	2.84 ± 0.39	56.13
Total	110	100.00	1–9	293	4.67 ± 0.28	2.57 ± 0.28	55.03

[a] Different superscript letters in the same column indicate significant differences (*t-test*, $P < 0.05$).

Table 2

Frequency of different *Microtus fortis calamorum* litter sizes in the laboratory.

Litter size	1	2	3	4	5	6	7	8	9	Total
Frequency	9	27	39	53	76	41	36	9	3	293
Percent (%)	3.07	9.22	13.31	18.09	25.94	13.99	12.29	3.07	1.02	100.00

survival rate of offspring to weaning was 55.03%. The primary cause of mortality was infanticide by the parents. The mean number of pups surviving in each litter was 2.57 ± 0.13, so the reproductive index of the lab population was 3.42 when based on pup survival. This means that the population could multiply 3.42 times during 3 months in the laboratory.

3.2. Reproductive characteristic of different parities

The mean litter size of different *M. f. fortis* parities, mean farrowing interval, and frequency of farrowing interval were calculated (Tables 3–5). The average litter size was significantly different between parities (One-way ANOVA: $F_{3,289} = 9.918$, $P < 0.001$) and the average litter sizes of the first and second litters were smaller than those of the third and fourth litters (Table 5). The mean farrowing interval differed significantly ($F_{3,289} = 5.441$, $P = 0.01$) between parities. The longest mean interval was for the first litter, and the mean farrowing interval decreased with successive parities. The shortest farrowing interval was for the fourth litter (Table 3). The farrowing intervals with the greatest frequency were 23 days for the first litter and 21 days for subsequent litters (Table 4). The weaning rates of offspring did not differ among parities (Pearson Chi-Square: $\chi^2 = 4.791$, $df = 3$, $P = 0.188$; Table 5).

Table 3

Mean farrowing interval for different birth sequences of *Microtus fortis calamorum* in the laboratory.

Farrowing sequence	Sample size	Farrowing interval range (days)	Farrowing interval (mean ± SE) (days)[a]
First litter[b]	96	21–95	28.6 ± 1.4^a
Second litter	91	20–61	26.2 ± 1.0^{ab}
Third litter	68	20–44	23.3 ± 0.5^b
Fourth litter	38	19–53	22.7 ± 0.9^b
Total	293	19–95	25.9 ± 0.6

[a] Different superscript letters in the same column indicate significant differences (*t-test*, $P < 0.05$).
[b] The mean farrowing interval of the first litter means the interval between pairing and birth of the first litter.

3.3. Reproductive parameters of 30 dissected breeding pairs

Among the 30 dissected pairs, the average number of embryos was 5.54 ± 0.45 ($n = 26$). The number of embryos varied from 1 to 8. The mean number of embryos was significantly greater than the mean litter sizes of the first ($t = 4.373$, $df = 120$, $P < 0.001$) and second ($t = 2.451$, $df = 115$, $P = 0.016$) litters as seen in Table 5. However the mean number of embryos was similar to the mean litter sizes of the third ($t = 0.744$, $df = 92$, $P = 0.459$) and fourth ($t = 0.021$, $df = 62$, $P = 0.983$) litters, which tended to be the largest. The pregnancy rate of dissected females was 86.7%, which was close to the overall population pregnancy rate of 87.3% ($\chi^2 = 0.009$, $df = 1$, $P = 0.926$). The reproductive index was 2.40.

3.4. Reproductive parameters after removal of males

After the males were removed from each cage, females might give birth if they had become pregnant before separation. Of the 80 lone females, 42 females produced a litter, and the average number of pups in each litter was 5.12 ± 0.32 ($n = 42$). The number of litter sizes varied from 1 to 9. Mean litter size was close to that of the fourth litter ($t = 0.854$, $df = 78$, $P = 0.396$; Table 5), and was significantly larger than that of the first litter ($t = 3.651$, $df = 136$, $P < 0.001$; Table 5). The mean farrowing interval was 24.6 days, which is close to the overall farrowing interval (25.9 days; $t = 0.805$, $df = 333$, $P = 0.422$; Table 3), and significantly different from that of the first litter (28.6 days) ($t = 2.202$, $df = 136$, $P = 0.030$; Table 3). The longest interval between separation and parturition was 19 days (5 litters). Infanticide was more common after removal of males from cages than it was when males were present (Table 6). The survival rate of offspring to weaning was significantly lower when no males were present in cages than it was when both parents were present in the cage (Pearson Chi-Square: $\chi^2 = 52.756$, $P < 0.001$). The rate of survival to weaning in the absence of males was also significantly lower than that of any of the 4 previous litters (first litter: $\chi^2 = 43.006$,

Table 4
Frequency of different farrowing intervals for *Microtus fortis calamorum* in the laboratory.

Farrowing interval (days)	Frequency	Percentage (%)	Cumulative percentage (%)	Frequency of farrowing intervals by different litters[a]			
				The first litter	The second litter	The third litter	The fourth litter
19	2	0.7	0.7				2(5.3)
20	11	3.8	4.4		3(3.3)	5(7.4)	3(7.9)
21	75	25.6	30.0	4(4.2)	36(39.6)	21(30.9)	14(36.8)
22	59	20.1	50.2	13(13.5)	19(20.9)	20(29.4)	7(18.4)
23	54	18.4	68.6	33(34.4)	7(7.7)	7(10.3)	7(18.4)
24	21	7.2	75.8	16(16.7)	1(1.1)	3(4.4)	1(2.6)
25	14	4.8	80.5	9(9.4)	1(1.1)	3(4.4)	1(2.6)
26	4	1.4	81.9		2(2.2)	1(1.5)	1(2.6)
27	5	1.7	83.6		2(2.2)	2(2.9)	1(2.6)
28	4	1.4	85.0	1(1.0)	2(2.2)	1(1.5)	
29	4	1.4	86.3	2(2.1)	2(2.2)		
30	1	0.3	86.7	1(1.0)			
31	2	0.7	87.4	1(1.0)	1(1.1)		
32	1	0.3	87.7		1(1.1)		
33	1	0.3	88.1			1(1.5)	
35	1	0.3	88.4	1(1.0)			
36	2	0.7	89.1	1(1.0)	1(1.1)		
37	4	1.4	90.4	1(1.0)		3(4.4)	
40	3	1.0	91.5	1(1.0)	2(2.2)		
41	2	0.7	92.2		2(2.2)		
42	1	0.3	92.5		1(1.1)		
44	1	0.3	92.8			1(1.5)	
45	3	1.0	93.9	1(1.0)	2(2.2)		
46	1	0.3	94.2	1(1.0)			
47	1	0.3	94.5	1(1.0)			
48	1	0.3	94.9	1(1.0)			
49	3	1.0	95.9		3(3.3)		
50	2	0.7	96.6	2(2.1)			
53	2	0.7	97.3	1(1.0)			1(2.6)
60	1	0.3	97.6		1(1.1)		
61	2	0.7	98.3		2(2.2)		
62	1	0.3	98.6	1(1.0)			
70	1	0.3	99.0	1(1.0)			
73	1	0.3	99.3	1(1.0)			
76	1	0.3	99.7	1(1.0)			
95	1	0.3	100.0	1(1.0)			

[a] The numbers in parentheses indicate the percentage of the total number of intervals of a particular duration in each litter sequence

Table 5
Reproductive characteristics of different parities of *Microtus fortis calamorum* in the laboratory.

Parities	No. of breeding females ($n = 110$)	Total offspring	Mean litter size (mean $\pm$ SE)[a]	Total surviving offspring	Mean no. offspring per litter surviving to weaning	Weaning rate of offspring (%)[b]
First litter	96	392	4.08 ± 0.13[a]	220	2.29 ± 0.19	56.12[a]
Second litter	91	413	4.54 ± 0.18[a]	215	2.36 ± 0.24	52.06[a]
Third litter	68	354	5.21 ± 0.22[b]	209	3.07 ± 0.29	59.04[a]
Fourth litter	38	210	5.53 ± 0.36[b]	109	2.87 ± 0.43	51.90[a]

[a] Different superscript letters in the same column indicate significant differences (*t*-test, $P < 0.05$).
[b] Different superscript letters in the same column indicate significant differences (χ^2, $P < 0.05$).

Table 6
Survival of *Microtus fortis calamorum* offspring to weaning with and without paternal presence.

Social condition during lactation	Total offspring	No. offspring surviving to weaning	Survival rate of offspring (%)[a]
Both parents present	1369	753	55.0[a]
Only mother present	215	61	28.4[b]

[a] Different superscript letters in the same column indicate significant differences (*Pearson chi-Square*, $P < 0.001$).

$P < 0.001$; second litter: $\chi^2 = 32.202$, $P < 0.001$; third litter: $\chi^2 = 50.452$, $P < 0.001$; fourth litter: $\chi^2 = 24.513$, $P < 0.001$).

4. Discussion

Seasonal reproduction is common among mammals. In photoperiodic rodents, long days generally stimulate reproduction, whereas short days generally inhibit reproduction. Whereas, there are some species of rodent can override photoperiodic control, switching instead to opportunistic reproduction based on foraging conditions without selection acting against responsiveness to

Table 7

Reproductive capacity of *Microtus fortis calamorum* field populations in different habitats and seasons.[a]

Item	Habitats			Seasons			
	Lake beach	Paddy field	Hillock	Spring	Summer	Autumn	Winter
Period (Month)	November–May	May–October	January–December	February–April	May–July	August–October	November–January
Total no. of females	185	280	63	148	237	73	59
Number of pregnant females	95	57	8	96	10	21	16
Pregnancy rate (%)	51.4	20.4	12.7	64.9	4.2	28.8	27.1
Mean litter size (mean ± SE)	5.06 ± 0.15	5.37 ± 0.25	4.38 ± 0.57	5.46	3.50	4.57	3.44

[a] Adapted from Wu (1996) and Chen et al. (1998). Voles were trapped 1992–1994 and the pregnancy rate was not different between years.

day length (Bronson, 2009; Stevenson et al., 2009). Food availability and ambient temperature determine energy balance, and changes in energy balance are the ultimate cause of seasonal breeding in all mammals and the proximate cause in many (Bronson, 2009). Fox example, voles can exhibit reproductive elasticity and may breed in winter if environmental conditions enable them (Stevenson et al., 2009). The main breeding season in the wild population of Yangtze vole is from November to April when they are on the beaches of Dongting Lake (i.e., their preferred habitat), and they have very low breeding potential after they are forced to migrate onto farmland by summer floods (the flood season) (Wu et al., 1996). The vole differs from other local rodent species in that it breeds during the short days of winter, whereas all other rodent species in Dongting Lake area stop breeding or have low fertility in winter. Interestingly, the northern subspecies of the vole in China also exhibit high reproductive capacity only in summer (Wu et al., 1996). This means that the vole subspecies in China are not uniformly responsive to variations in photoperiod. Differences in breeding response to photoperiod among subspecies has also been observed in some American rodents, e.g., California voles (*Microtus californicus*) (Nelson et al., 1983), California mice (*Peromyscus californicus*) (Nelson et al., 1995), White-Footed Mouse (*Peromyscus leucopus*) (Lynch et al., 1981). Observations suggests that intra-species variation in photoresponsiveness is much more common in small rodents than previously thought (Lynch et al., 1981; Heideman et al., 1999; Bronson, 2009). The mechanism by which seasonal reproduction of the Yangtze vole is regulated is not yet known. Similarly, the reasons for the considerable intraspecific and interspecific variability of vole breeding responses to photoperiod are not understood. We therefore simply simulate the photoperiod experienced in the wild during the breeding season in our laboratory. As in the present study, the Yangtze vole breeds productively year round in captivity when exposed to a short photoperiod.

From the shortest farrowing interval in this study and the longest interval between separation and parturition, it can be estimated that the gestation of *M. f. calamorum* is approximately 19–21 days in the laboratory. This gestation period is very similar to that of other subspecies of *M. f. fortis* (Hu et al., 2003). The *M. f. calamorum* observed in this study had a shorter mean farrowing interval and larger mean litter size than a laboratory population of *M. f. fortis*

(25.9 vs. 39.3 days and 4.67 vs. 3.8, respectively) (Hu et al., 2003).

The laboratory population has similar reproduction parameters to those of field populations, except for pregnancy rate. Although pregnant females can be found during any month in the field, the pregnancy rate varies significantly between seasons. However, the overall pregnancy rate is 29.2% in the field (Wu et al., 1996; Chen et al., 1998). In the field, voles have high pregnancy rates from autumn to spring (the winter half of the year), when they inhabit the beaches (Table 7) (Wu et al., 1996; Chen et al., 1998). However, when the voles move to cropland in the summer, pregnancy rates plummet. This large drop in pregnancy rate is probably due to disturbances from floods, frequent disturbances associated with farming, high summer temperatures and long light cycle in summer in Dongting Lake region (Wu et al., 1996; Guo et al., 1999).

In the established laboratory population, the voles are able to breed throughout the year in a laboratory maintained at 20–22 °C under a 12L:12D light cycle. The litter size of the laboratory population ranges from 1 to 9, as does those of field populations (Wu et al., 1996). The mean litter size of the voles in the laboratory increased with increasing parity, which is consistent with an observed increase in fecundity with age in the field populations (Wu et al., 1996). The mean litter size in the field is 5.13 ± 0.12 (Mean ± SE). Although the mean number of pups per female varies substantially, but most litters include between 3 and 6 pups (Wu et al., 1996). In 3-month study, the mean litter size for all females was 4.67 ± 0.28, which is smaller than the mean litter size observed in the field. However, only the first and second pregnancies resulted in fewer than 5 pups per litter, on average. The mean litter sizes of the third and fourth litters were greater than 5 (Table 5), as was the mean litter size of females after males were removed from cages. The mean number of embryos in dissected females was also greater than 5. The slightly higher litter size reported for field populations may be based on embryo counts, which may not reflect the number of young at birth (Lötter and Pillay, 2008). In the present study, the mean number of embryos per litter among dissected females was higher (5.54 ± 0.45) than the mean number of pups born per litter although they were not significantly greater than the mean litter sizes of the third and fourth litters.

The examined laboratory population of Yangtze voles had similar reproduction parameters to some other *Microtus* species. The gestation period of the studied voles was

very similar to that of Russian voles (*Microtus rossiaemeridionalis*), which have a gestation period of 20.6 ± 0.9 (SD; range, 18–22 days; Widayati et al., 2003). The Yangtze vole gestation period was also similar to that of *Microtus montebelli, Microtus Montanus*, *Microtus oeconomus*, and *Microtus pennsylvanicus*, which have a gestation period of almost 21 days, and Hungarian voles (*Microtus arvalis*), which have a gestation period of 20 days (Kudo and Oki, 1984; Widayati et al., 2003). The mean litter size (4.67) of Yangtze voles in the laboratory population was similar to those of Russian voles (mean ± SD, 4.6 ± 1.9, range: 1–10; *n* = 125; Widayati et al., 2003), Japanese field voles (*M. montebelli*; 4.65 ± 1.39), Hungarian voles (4.75 ± 1.40; Kudo and Oki, 1984). However, the average litter size of the study population was large compared with some other *Microtus* species, such as *Microtus breweri* (3.3), *Microtus ochrogaster* (3.0–4.6), *M. oeconomus* (3.9), *Microtus pinetorum* (2.2–2.3) and *Microtus savii* (2.6; Widayati et al., 2003). In general, the litter size of Yangtze voles is relatively large compared to other *Microtus* species.

In both the field and the laboratory, the mean litter size of Yangtze vole increases as the population increases in age, with the oldest animals producing the largest litters. This is similar to *Niviventer confucianus* in the Dongting Lake region (Zhang et al., 2006) and *Phodopus roborovskii* in Inner Mongolia (Hou et al., 2000). This phenomenon has also been observed in Russian voles, for which first litters (3.6 ± 1.6) are smaller than subsequent litters (5.9 ± 1.4), up to the 7th litter (Widayati et al., 2003). The initial litters of *Microtus epiroticus* are also smaller than subsequent litters (Yoccoz et al., 1993). Such, litter size increases with age class or body weight and the production of the largest litter sizes by old-adult groups, may be common to many rodent species (Zhang et al., 2006).

Both male and female Yangtze voles are reported to engage in infanticide. Guo (1998) reported that 44.4% of sexually naïve males and 72.0% of sexually naïve females captured from a wild population exhibited infanticide, and 40.6% of males and 63.2% of females from the first and second laboratory generations spontaneously engaged in infanticide. In the present study, parent voles also killed their own offspring before weaning, as indicated by bite marks on most of dead pups, or some of which were only partial bodies. The high mortality rate after removal of males confirmed maternal infanticidal tendencies. This behavior has been observed in many rodents (König, 1989; Elwood, 1991; Mendl, 1994; Widayati et al., 2003; Weber and Olsson, 2008). There are five hypotheses commonly used to explain infanticide: exploitation, resource competition, parental manipulation, sexual selection, and social pathology (Hrdy, 1979). In most cases, maternal infanticide is evoked from by some "stressor". For example, female mice (*Mus musculus*) reduce litter size when food is restricted (König, 1989; Elwood, 1991). By doing so, dams could maintain high levels of maternal care and would not be sacrificing their future parental investment (Trivers, 1972). Many stressors, such as noise, olfactory, or physical disturbance, increases cannibalistic behavior by adult mice and rats (Poley, 1974; McCarthy and Saal, 1985; Reeb-Whitaker et al., 2001; Burn and Mason, 2008). Under these stressor, even though some species could not reduce the

size of their litters, they would show a decrease in maternal behavior toward pups or would be sacrificing their body condition and future parental investment (Trivers, 1972; Sabau and Ferkin, 2013a,b). It should be noted that infanticide is typically inferred from what is usually found is a reduced number of pups, or the presence of partially eaten pups in the cage, rather than observations of females actively killing pups. Therefore, maternal cannibalism may be a more appropriate term than infanticide (Weber and Olsson, 2008). We do not know why the Yangtze voles kill their own offspring, or the benefits of infanticide to female voles. From the relatively high proportion of pups killed after the removal of males in the present study, we speculate that females may have been adjusting the number of pups in the litter. Similar findings have been reported in other rodents, for instance mice (Gandelman and Simon, 1978), golden hamsters (Day and Galef, 1977). Rearing offspring requires parental investment (Trivers, 1972). The metabolic energy requirements of Pine voles (*Microtus pinetorum*) are approximately 47.5% greater than those of non-breeding females throughout the 21 days of lactation and there is a positive relationships between metabolizable energy intake and litter size (one to three young) (Lochmiller et al., 1982). Thus, in reduced litters, increases in parental attention to the few remaining pups may increase their subsequent quality (Mendl, 1994).

Voles are altricial rodents, and both male and female parents typically invest parental care in their offspring. For example, the growth of Mandarin vole (*Microtus mandarinus*) pups with an absent father is poorer than that of pups with both parents present due to relatively low parental investment (Song et al., 2010; Wang et al., 2011). Female reproductive success may be limited by the loss of male parental investment (Trivers, 1972). McGuire et al. (1992) examined the effects of removing males on pregnancy success in prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*), two species that differ in the degree of paternal investment; prairie vole males provide extensive care to offspring and pup development is relatively fast, whereas meadow vole males provide little or no care and pup development is delayed. Accordingly, removal of males soon after mating decreased pregnancy success in prairie voles and increased pregnancy success in meadow voles. In the present study, the percentage of pups surviving to weaning when raised by the female parent alone was half that of pups raised by both parents (Tables 1 and 6). The relatively low rate of offspring survival after the removal of males indicates that high reproductive success requires the presence of both parents in the laboratory.

Here, we reported the reproductive characteristics of the Yangtze vole. This basic information is necessary in order to develop the vole into a model species. Many *Microtus* species have been suggested as candidates for small laboratory animal models of large domestic ruminants (Dieterich and Preston, 1977a,b; Kudo and Oki, 1984; Widayati et al., 2003) because they have strong herbivorous features as characterized by a complex stomach and possession of cellulolytic bacteria (Kudo and Oki, 1984). For example, Japanese field voles and Hungarian voles have been used as herbivorous experimental

animals (Kudo and Oki, 1984). *Microtus* species are polyestrus, show postpartum estrus on the day of parturition, and have little or no delay in implantation due to lactation (Kudo and Oki, 1984). Therefore, voles are able reproduce quickly in the laboratory. Sabau and Ferkin (2013b) also found female *Microtus pennsylvanicus* come into postpartum estrus within 12–24 h of giving birth, allowing them to mate and become pregnant while raising the current litter. In the present study, the mean farrowing interval of Yangtze voles (including the interval between pairing and birth of the first litter) was 25.9 days and the shortest farrowing interval was 19 days (Table 4), which indicates that the voles were probably in estrus soon after parturition. More importantly, because the Yangtze vole is the only known mammal species with natural resistance to schistosomiasis (Zhu et al., 1991; He et al., 1999a,b; Li et al., 2001), it is worth developing as a laboratory animal. With the exception of a high rate of infanticide, the population of Yangtze voles in our laboratory has adapted successfully to laboratory conditions.

Acknowledgments

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