Inter- and intraspecific diversity of ontogeny and fecundity patterns in relation to reproductive strategy choice in Myomorpha (Rodentia: Calomyscidae, Cricetidae, Muridae)

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ORIGINAL PAPER

Inter- and intraspecific diversity of ontogeny and fecundity patterns in relation to reproductive strategy choice in Myomorpha (Rodentia: Calomyscidae, Cricetidae, Muridae)

Kordiyeh Hamidi[1] · Maryam M. Matin[1,2] · Jamshid Darvish[1,3] · Vladimir G. Malikov[4]

Abstract

Studying the life history of various organisms is essential for ecological and evolutionary inferences. However, publications regarding models of evolutionary shifts to either r- or K-reproductive strategies are scarce. Here, the combined original and previously published data on reproduction and development of Goodwin's brush-tailed mouse (*Calomyscus elburzensis*), golden hamster (*Mesocricetus auratus*), and house mouse (*Mus musculus*) were compared. An adult male and female in estrous state (from each species) were coupled with each other for a night and embryos were harvested at embryonic days (E) 10–17 from pregnant females. The mean gestation period in Goodwin's brush-tailed mouse was 31.5 ± 2.1 days; growth was rapid at the first half of this period and after that it was reduced by half. During the postnatal period, growth was rapid up to weaning, but after day 35, the rate of growth decreased abruptly. Growth rate of head and body length was very rapid prior to weaning (PN35) in comparison with weight but the rates of the two characters were inversed following weaning. Totally, weight gain was more dynamic in rate, as compared with head and body length, up to adultness. For golden hamster and house mouse, gestation period was 15.6 ± 0.8 and 20.8 ± 0.8 days, respectively. Growth was slow during approximately the first half of the gestation period in both species but increased during the second half. During postnatal period in golden hamster, growth rate of head and body length was rapid both before and after weaning as compared with that of weight. However, head and body length showed a stable rate of growth before and after weaning (around PN15), but for body weight, the growth rate was slightly faster after weaning. Similarly, changes in head and body length in house mouse were rapid both before and after weaning (PN16) as compared with that of weight. Since approximately two-fold increases were observed in the growth rates of weight and head and body length in the second stage of postnatal development (PN16-adult) compared with the rates during the first stage (PN0-PN16), both showed dynamic changes during the postnatal development in this species. Typically, r-strategic house mouse appeared to be more similar in early morphological development to comparatively K-strategic Goodwin's brush-tailed mouse, than to comparatively r-strategic golden hamster. Nevertheless, growth rate and pattern were different in the three species after birth. Hence, results showed that peculiarities of association between an ontogenetic pattern and a tendency in reproductive strategy can differ in diverse groups of myomorph rodents.

Keywords Ontogeny · Pre- and postnatal development · Reproductive strategy · *Mus* · *Mesocricetus* · *Calomyscus* · Arvicolini

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Jamshid Darvish is deceased. This paper is dedicated to his memory.

Communicated by: Shuiqiao Yuan

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Introduction

Traditional scenarios of higher vertebrate evolution are most often based on assessment of similarities in adult morphology of living and fossil forms. However, the basic approach of "evolutionary developmental biology (*Evo-Devo*)" is that evolutionary changes are the result of ontogenetic pathways rather than changes occurring after birth (Creighton and Strauss 1986; Eilam 1997; Wilson 2011). Although several studies have documented the variability and evolution of ontogenetic allometry (Fadda and Leirs 2009), heterochronic patterns (Weston 2003; Cubo et al. 2006; Zollikofer and de León 2010), or growth patterns among species and intraspecific clades (Cardini and O'Higgins 2005; Marroig 2007; Wilson and Sánchez-Villagra 2010) in mammals, all have focused on the postnatal period of development. Early ontogenetic stages have been ignored despite their important role on adult state (Bastir and Rosas 2004; Bulygina et al. 2006; Wilson et al. 2008; Wilson and Sánchez-Villagra 2010).

In mammals, the relationship between pre- and postnatal development as well as the evolutionary role of prenatal ontogeny is limited to studies of humans and other primates (e.g., Bastir and Rosas 2004; Vinicius 2005; Sardi et al. 2007). One reason for this is the difficulty in obtaining prenatal series for any mammal with the sample size required to assess precise relationships (Sánchez-Villagra 2010). This is particularly acute with rodents in which it is difficult to obtain embryos at early stages of prenatal development due to the small size of the embryos. For this reason, precise determination of conception is needed but is extremely difficult to obtain. However, comprehensive data on reproduction and/or comparative ontogenesis are available (Asdell 1946; Creighton and Strauss 1986; Hayssen et al. 1993; Eilam 1997; Kaufmann and Bard 1999; Kaufmann 2008; Olio et al. 2014) which make it possible to model evolutionary events, including shifts in reproductive strategy.

Life history studies explain how organisms adapt to achieve reproductive success. The major features of life history are age-structured reproduction and survival including age and size at maturity, length of reproductive lifespan, reproductive investment, mean fertility, and aging which can be influenced by changes in the environment such as resource availability and environmental fluctuations (Stearns 2000; Reznick et al. 2002; Dobson and Oli 2008). Pianka (1970) mentioned some elements to distinguish two main groups of life histories known as Pianka's correlates of *r*-selection and *K*-selection including climate, population size, inter- and intraspecific competition, relative abundance, and longevity. Ontogenetic variations observed among species (or higher taxa) are cues leading to understanding life history traits, often based on some characteristics such as rapid development, short-lived, and high fecundity (*r*-strategy) versus slow development, long-lived, and low fecundity (*K*-strategy).

Therefore, the *r*- or *K*-strategies are known to be two opposite adaptive scenarios of survival (Dobzhansky 1950; MacArthur and Wilson 1967; Reznick et al. 2002).

In reality, no organism is completely "*r*-selected" or completely "*K*-selected" but all must reach some compromise between the two extremes (Pianka 2000). According to Fisher (1930), "it would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction."

The house mouse, *Mus musculus* Linnaeus, 1758 (Rodentia: Muridae), is the most common model system for mammalian development (Zelditch et al. 2003b). This species displays a typical *r*-reproductive strategy, being able to produce tremendous numbers of offspring resulting in outbreaks of populations with high densities (Weber and Olsson 2008). The golden or Syrian hamster, *Mesocricetus auratus* (Waterhouse, 1839) (Rodentia: Cricetidae), another animal model, is easy to breed in captivity, so it is used in laboratories for broad fields of research (Valentine et al. 2012). The laboratory stocks of this species can display a typically *r*-kind of reproduction. Although no evidence of population explosions have been reported in the wild, they are considered a major agricultural pest within their native range and are subjected to extensive annual exposure to rodenticides (Gattermann et al. 2001) which appears to have resulted in population declines (Yigit and Kryštufek 2008). Brush-tailed mice (Rodentia: Calomyscidae) are a group of small-sized rodents found in rocky outcrops and semi-mountainous areas in desert regions of Syria, Azerbaijan, Iran, Turkmenistan, Afghanistan, and Pakistan (Musser and Carleton 2005; Kilpatrick 2017). With a mouse-like exterior and ecotype, that appears to be a common morphology of rodents, brush-tailed mice are known to have a life span of over 9 years in captivity (Volf and Volf 2003), second only to the slender-tailed cloud rat, *Phloeomys cumingi* (Waterhouse, 1839), which is reported to have a maximum lifespan of 13 years in captivity (Denys et al. 2017). These rodents are also characterized by a comparatively slow rate of postnatal development and a low fertility rate (Meyer and Malikov 1996; Kilpatrick 2017). There are no data on prenatal life history of this group and the only embryology reference is Hamidi et al. (2017b).

The aim of the present study was to describe changes in growth and development which take place during pre- and postnatal stages of Goodwin's brush-tailed mouse (*Calomyscus elburzensis* Goodwin, 1939) in comparison with the house mouse and the golden hamster. For this purpose, the following items were considered: (1) comparative stages of pre- and postnatal development in Goodwin's brush-tailed mouse, house mouse, and golden hamster, and (2) the fecundity in laboratory

stocks of the three species as well as some voles including their ontogenetic and reproductive extremes which were "pulled out" from the "bottle-necked" origins of captive breeding colonies. Most laboratory stocks originated from very few parental individuals, and hence, the effects of inbreeding are inevitable. In such situations, some characteristics (for example, alternative reproductive parameters to those observed in wild populations), which are hidden by genetic polymorphism of natural populations, can be revealed (Meyer and Malikov 1996; Olenev 2002).

Materials and methods

Animal capture and breeding

The Goodwin's brush-tailed mice (12 adult males and 15 adult females, average weight 19.0 g) used in this study were captured from various localities in the northeast of Iran using custom-made mesh live traps (Hamidi et al. 2015). Furthermore, 10 male and 10 female Soori albino house mice (4-week-old and with average weight 26.0 g) and golden hamsters (3-week-old and with average weight 29.0 g) were purchased from Razi Vaccine and Serum Research Institute of Mashhad, Iran. The animals were housed in separate cages in a room with a 12-h light and dark cycle, with temperature of 24–28 °C, and 25–35% humidity. Brush-tailed mice received a variety of seeds and fruits similar to their natural diet, whereas house mice and golden hamsters were fed with standard mouse feed pellets and water ad libitum throughout the experiments. An adult male and female in estrous state (from each species) were coupled with each other for a night, in a cage separately from others. Although there are no data on the estrous cycle for brush-tailed mice, there are some common signs in rodents that are useful in determining when females are in estrous, including holding the tail up, changing in the appearance and color of the vaginal area from pink to reddish, tendency towards males with showing less aggressive manner, and dispersing special smells (Champlin et al. 1973; Marcondes et al. 2002). The following morning, if possible, vaginal smears were prepared and examined under a light microscope to determine the presence of sperms and probable subsequent pregnancy. If pregnancy occurred, counting the embryonic days (E) was started, with E0 indicating the first day after separating female from male. In addition, the animals were observed daily and their body weight was recorded three times a week to verify pregnancy, normal growth, and well-being of the embryos. Pregnant females (6 Goodwin's brush-tailed mice, 6 golden hamsters, and 8 house mice) were placed in different cages during their pregnancy. Embryos were obtained from euthanized females at days E10–17. Furthermore, newborn pups of each species at different postnatal days (PN) were included in the study (see Hamidi et al. 2018 for details). Animal care and experimental procedures were performed in accordance with the guidelines and protocols approved by the ethics committee of the Rodentology Research Department, Ferdowsi University of Mashhad.

Measurements

External measurements used in this study including head and body length, tail length, total body length, and hind foot length were taken with a vernier caliper with an accuracy of 0.1 mm. After the birth of newborns, the total body weights of pups were taken daily with an accuracy of 0.1 g and embryo weights were recorded for each stage examined. Data were also recorded on the mean length of the gestation period and on the timing of developmental events including eye opening, ear eruption, weaning (called as "juvenile" from now on), and starting to feed. These events also correspond with phases of ontogenesis in rodents, such as attainment of the abilities to orient to their environment acoustically or visually and to process solid food. For all recorded values, standard deviation (SD) was provided as a measure of the amount of variability or dispersion of the data from the mean.

Results

Gestation period in Goodwin's brush-tailed mouse was 31.5 ± 2.1 days on average. The average gestation period in golden hamster was 15.6 ± 0.8 days, which was 5 days shorter than that of the house mouse (20.8 ± 0.8). The average mothers' weights prior to parturition were 28 ± 1.4, 97.8 ± 1.4, and 56.2 ± 1.6 g in Goodwin's brush-tailed mouse, golden hamster, and house mouse, respectively. The reproductive cycle in Goodwin's brush-tailed mice was approximately 1 litter every 9 months. Females in northeastern Iran produce offspring from late winter (in nature) and late autumn (in captivity) until late spring (Hamidi et al. 2015). There are insufficient data for litter size in nature with only a record of two wild females collected in November which had 2 and 7 uterine swellings with no visible embryos (Lay 1967). However, the number of young per litter in captivity has been well-studied; captive females generally produced 1 to 5 (3 ± 1.5) young in each parturition (Hamidi et al. 2018). True hamsters and domestic mice reproduce throughout the year and the number of offspring per litter was 8.6 ± 1.5 and 11 ± 2.5, respectively (Table 1).

Morphology and size in prenatal period

At E13, embryos of Goodwin's brush-tailed mouse weighed on average 0.2 ± 0.02 g, and total body length measured 7.1 ± 0.1 mm. Ears and eyes were not distinguishable and head and limbs showed very little development (Fig. 1, Table 2). At E14, weight and head and body length were 0.3 ± 0.01 g and

Table 1 Comparative reproductive features of Goodwin's brush-tailed mouse (*Calomyscus elburzensis*), golden hamster (*Mesocricetus auratus*), and house mouse (*Mus musculus*). Some parts reproduced from Suckow et al. (2000), Volf and Volf (2003), Banks et al. (2010), and Hamidi et al. (2017b, 2018) are shown in italics and are indicated with ▪, ♦, •, *, and **, respectively. For all recorded values, standard deviation (SD) is provided

Developmental characteristic	Species		
	Calomyscus elburzensis	*Mesocricetus auratus* (Lab race)	*Mus musculus* (Lab race)
Age of sexual maturity	*Not less than 4 months of age for both females and males* **	*Females at 6 weeks of age and males at 8 weeks* •	*Females at about 6 weeks of age and males at about 8 weeks* ▪
Length of the gestation period (day)	*31.5 ± 2.1* *	*15.6 ± 0.8* *	*20.8 ± 0.8* *
Mean number of litters/year	One litter every 9 months	Every month throughout the year	Throughout the year; 5 to 10 litters per year
Mean number of young/litter	3 ± 1.5	8.6 ± 1.5	11 ± 2.5
Size (weight, and head and body length) of newborns	*2 ± 0.1 g* **, 30 ± 0.8 mm	2.8 ± 0.07 g, 31.8 ± 0.8 mm	2.4 ± 0.08 g, 31.4 ± 1.1 mm
Size (weight, and head and body length) of juveniles (at weaning)	16.7 ± 0.5 g, 59.1 ± 0.3 mm	17.9 ± 0.8 g, 70.1 ± 0.5 mm	12.7 ± 0.3 g, 64.5 ± 0.9 mm
Size (weight, and head and body length) of adults	19.7 ± 0.9 g, 76.5 ± 1.2 mm	72.2 ± 0.5 g, 149.6 ± 1.7 mm	27.5 ± 0.4 g, 85.7 ± 0.9 mm
Length of life span in captivity	*Generally between 4 to 5 years* ** *but there are records indicating that they can live as long as 9 years in captivity* ♦	*Mean 2–3 years, up to 4 years* •	*Normally for about 2 to 3 years but up to 5 years is also recorded* ▪
Reproductive strategy	Tendency to *K*-kind	A typical *r*-kind	A typical *r*-kind

9.1 ± 0.2 mm, respectively. Eyes were observed as a dark spot (pigmented optic vesicle) but ears were not completely obvious yet. Tail had grown as a very short appendage, and head development was more than that of limbs (Fig. 1). At E15, weight and head and body length showed 0.2 g (0.5 ± 0.01) and 4 mm (13.1 ± 0.1) increases, respectively. Ears were distinguished and the embryos were miniature newborns (Fig. 1). Embryos at E17 averaged 0.7 ± 0.01 g in weight and 19.1 ±

0.1 mm in head and body length. Growth was rapid during the first half of the gestation period (Fig. 2). Up to about E17, the embryos gained as much as 0.16 ± 0.01 g/day and 4 ± 0.1 mm/day and after that, in the second half of the gestation period until parturition, their growth rate decreased about half (0.09 g/day and 2.4 mm/day).

In the golden hamster, embryos at embryonic day 10 weighed on average 1.2 ± 0.05 g, and head and body length measured 11 ± 0.9 mm. Embryos had distinguishable ears and well-developed pigmented optic vesicles. Shallow grooves indicating the beginning of digit formation were observed on the fore and hind limbs (Fig. 3 and Table 2). At E13, weight and head and body length were 2.2 ± 0.02 g and 22 ± 0.5 mm, respectively. Fore and hind limbs showed elongation (Fig. 3). Growth was slow in the first two-thirds of the gestation period (up to E10), with embryos gaining only 0.12 ± 0.01 g/day and 1.1 ± 0.09 mm/day. However, in the last third of gestation, embryos grew rapidly at three to four times the rate of the first period for weight and head and body length, respectively (0.32 g/day and 4 mm/day) (Fig. 2).

House mouse embryos at E10 weighed on average 0.1 ± 0.09 g and total body length measured 6.8 ± 0.2 mm. Embryos had a distinguishable cephalic region and little development of the limbs, but a pronounced tail (Fig. 4). At E13, weight and head and body length were 0.3 ± 0.03 g and 10 ± 0.3 mm, respectively. Fore and hind limbs showed elongation, although faster development of the head as compared with the limbs was observed. Ears and eyes were not clearly distinguishable (Fig. 4 and Table 2). At E14, embryos weighed on average 0.5 ± 0.05 g and head and body length measured 10.4 ± 0.3 mm. External ears were forming and very weak pigmented optic vesicles and shallow grooves indicating the beginning of digit formation could be observed (Fig. 4). At E15, weight and head and body length were 1.1 ± 0.2 g and 17 ± 0.8 mm, respectively. External ear showed further projection with ear canal covered by the pinna (Fig. 4). At E17, embryos weighed on average 1.3 ± 0.2 g and head and body length measured 20.5 ± 0.7 mm with longer fore and hind limbs having separated digits (Fig. 4). Growth was slow during the first half of the gestation period (Fig. 2). Up to about E10, the embryos gained only 0.01 ± 0.01 g/day and 0.6 ± 0.1 mm/day but after that, in the second half of the gestation period, weight increased rapidly (0.23 g/day) and for head and body length, this was at about four times the rate observed in the first half of the gestation period (2.5 mm/day).

Morphology and size in postnatal period

At birth, brush-tailed mice, weighed on average 2 ± 0.1 g, had a head and body length of 30 ± 0.8 mm (Table 1) and were covered with a very thin and fine coat of dark-colored hair. Ears were separated from the head (Table 2) and the digits of the fore and hind limbs were separated from each other. By the
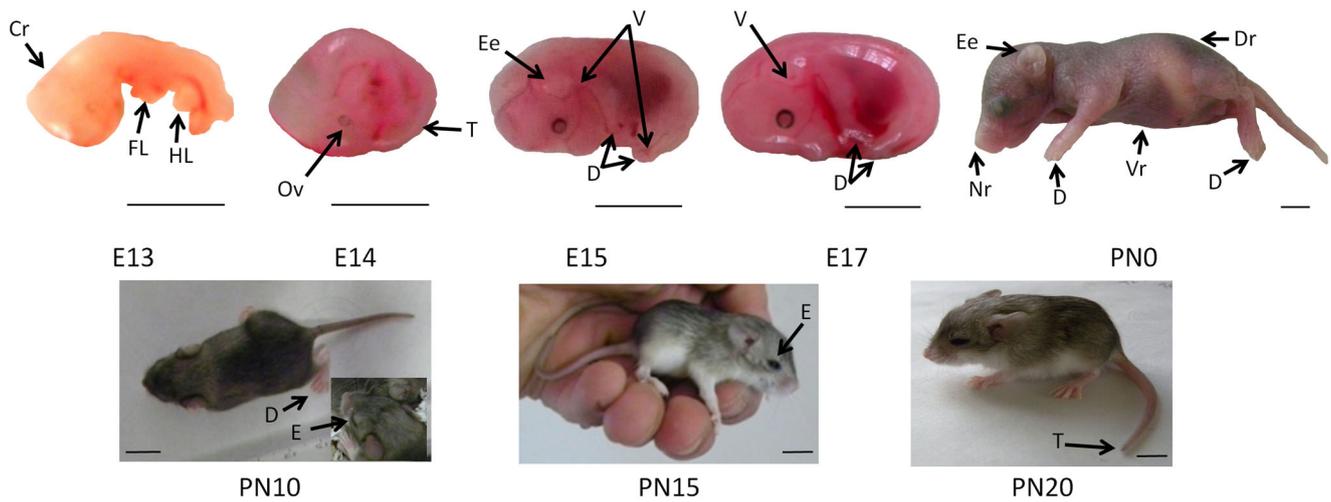
Fig. 1 *Calomyscus elburzensis* at embryonic days (E) 13, 14, 15, 17, and at postnatal days (PN) 0, 10, 15, and 20. E13: a distinguishable cephalic region (Cr), not distinguishable ears and eyes, formation of fore and hind limbs (FL and HL, respectively). E14: weak pigmented optic vesicle (Ov), slightly pronounced tail (T). Head development was more than that of limbs. E15: forming external ear (Ee) and ear canal covered by the pinna. Shallow grooves indicating the beginning of digit formation (D). The vascularization (V) was visible over the body due to little skin pigmentation. E17: peripheral vessels (V) can be observed through the thin skin, longer fore limbs and hind limbs with separated digits (D). PN0: a marked change in skin pigmentation, with a darker dorsal region (Dr) and lighter ventral region (Vr), further projected external ear (Ee), well-developed nasal region (Nr) and vibrissae. Separated digits with early formation of claws were visible at the ends of the fore and hind limbs (D). PN10: the eyes were still covered by a layer of skin (E), deeper grooves were visible between the digits (D). PN15: opening of eyes (E). PN20: individuals exhibited similar features to neonates, with elongated, well-developed bodies and longer tails (except in the tail tuft) (T). Scale bars indicate 5 mm in upper row and 10 mm in lower row

fifth day, the hair was erect and the dorsal regions of the head, body, and tail were generally dark gray, while the pelage of the undersurfaces was white (Table 2 and Fig. 1).

The body mass of the newborn was only 10.5% of the adult mass (19.7 ± 0.9 g) and increased to approximately 89.4% of the adult in juveniles (16.7 ± 0.5 g) at PN35. Growth was rapid; the young gaining as much as 0.6 g/day and at 15 days of age had reached 63.1% of the adult weight (12.4 ± 0.5 g). Head and body length in newborns was about 38.9% of the adult length (76.5 ± 1.2 mm) but doubled by the juvenile

Table 2 Major events in the pre- and postnatal developmental stages of Goodwin's brush-tailed mouse (*Calomyscus elburzensis*), golden hamster (*Mesocricetus auratus*) and house mouse (*Mus musculus*). E and PN indicate the average embryonic and postnatal days, respectively. Parts shown in italic are reproduced from Hamidi et al. (2018)

Developmental stage	Developmental feature	Species		
		Calomyscus elburzensis	*Mesocricetus auratus* (Lab race)	*Mus musculus* (Lab race)
Prenatal period	Forming of limbs	E15	Before E10	E13
	Distinguishing of ears	E15	Before E10	E14
	Distinguishing of fingers	E15	Before E10	E14
	Miniature newborn	E15	Before E10	E14
Postnatal period	Separation of ears from the head	*PN0*	PN3	PN2
	Emerging of thin hairs	PN1	PN2	PN2
	Primary erecting of hairs	PN3	PN4	PN4
	Opening of eyes	*PN15*	PN14	PN13
	Feeding on hard foods	After about PN24	PN14	PN14
	Weaning	*At about PN35*	PN15	PN16
	Beginning to explore outside the nest	*At about PN35*	PN15	PN15
	Miniature adult	After PN35 (when tail tuft appears)	PN15	PN15

a

b
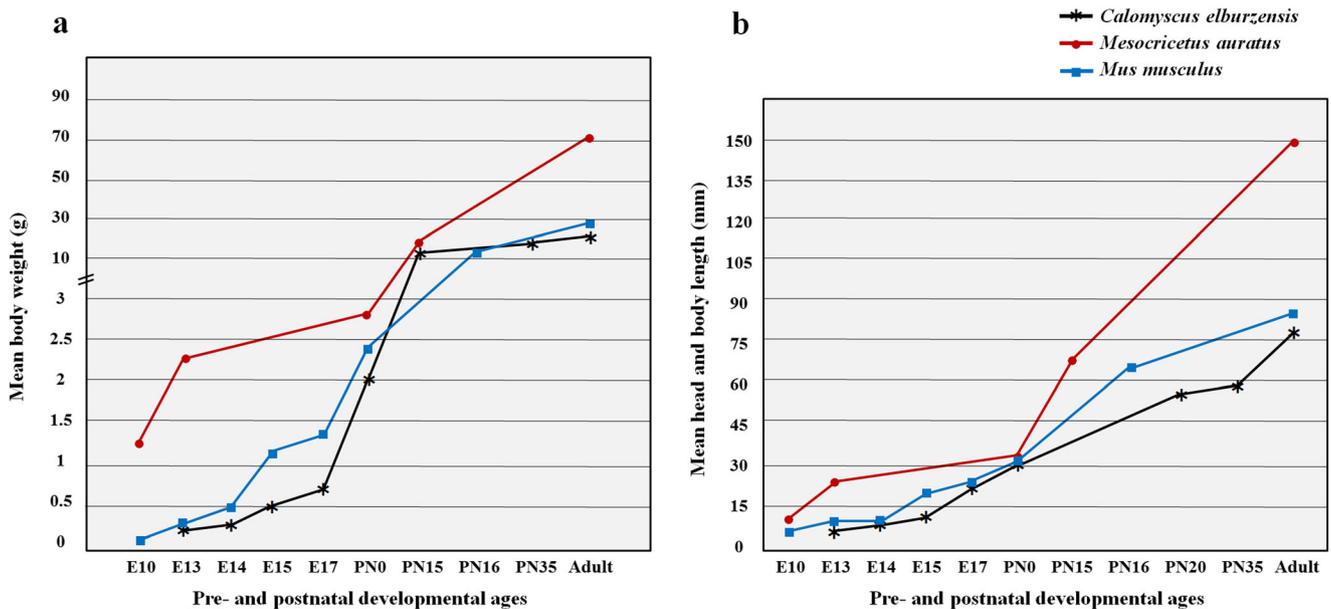
Fig. 2 Growth curves of Goodwin's brush-tailed mouse (*Calomyscus elburzensis*), golden hamster (*Mesocricetus auratus*) and house mouse (*Mus musculus*) during pre- and postnatal development. Changes in body weight (**a**) and head and body length (**b**) are shown for different E and PN, indicating the average embryonic and postnatal days, respectively. In Goodwin's brush-tailed mouse, prenatal growth was rapid at first half of gestation period (up to about E17) and after that, it grew slowly. Postnatal growth rate of head and body length was considerably rapid before weaning (PN35) as compared with that of weight, but this was inversed after weaning. Although, great increases were observed in the growth rate of weight, growth rate of head and body length during PN35 to adult showed little increase. In golden hamster,

prenatal growth was slow at first two-thirds of gestation period (up to E10) and after that, it grew rapidly. Postnatal growth rate of head and body length was rapid both before and after weaning (PN15) as compared with that of weight. However, no obvious changes were observed in the increasing rate of length in the first two stages of postnatal life (PN0-PN15 and PN15-adult). In house mouse, prenatal growth was slow at first half of gestation period (up to E10) and after that, it grew rapidly. Postnatal growth rate of head and body length was rapid both before and after weaning (PN16) as compared with that of weight. However, increasing was observed in the growth rate of both weight and length of body in the second stage of postnatal life (PN16-adult) as compared with the first one (PN0-PN16)
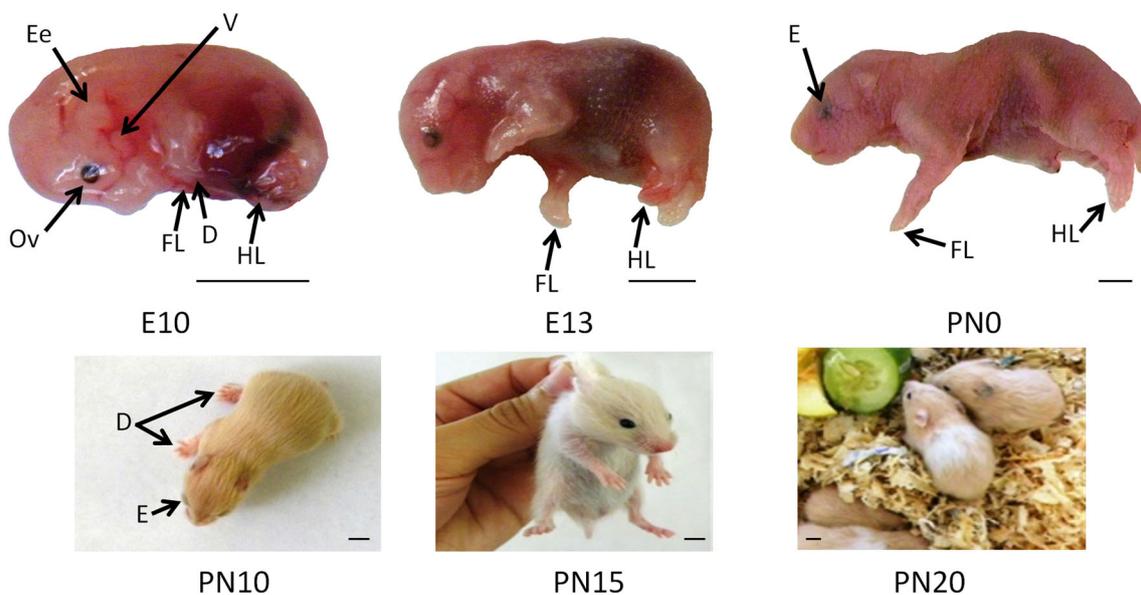
Fig. 3 *Mesocricetus auratus* at embryonic days (E) 10 and 13 and at postnatal days (PN) 0, 10, 15 and 20. E10: well development of pigmented optic vesicle (Ov), distinguishable external ear (Ee), developed fore and hind limbs (FL and HL, respectively). Shallow grooves indicating the beginning of digit formation (D). The vascularization (V) was visible over the body due to little skin pigmentation. E13: longer fore and hind limbs (FL and HL,

respectively). PN0: the eyes were still covered by a layer of skin (E), faster development of fore limbs (FL) as compared with hind limbs (HL). PN10: the eyes were still closed (E), deeper grooves were visible between the digits (D). PN15: weaning. PN20: individuals exhibited completely similar features to neonates. Scale bars indicate 5 mm in upper row and 10 mm in lower row
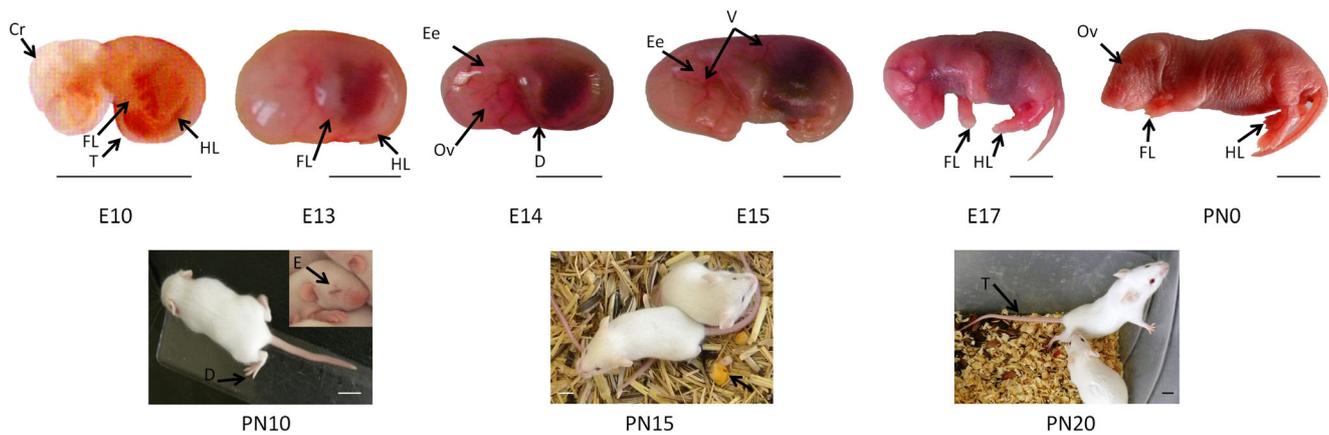
Fig. 4 *Mus musculus* at embryonic days (E) 10, 13, 14, 15, 17 and at postnatal days (PN) 0, 10, 15 and 20. E10: a distinguishable cephalic region (Cr), little development in fore and hind limbs (FL and HL, respectively), pronounced tail (T). E13: longer fore and hind limbs (FL and HL, respectively), not clearly distinguishable ears and eyes, faster development in the head as compared with the limbs. E14: very weak pigmented optic vesicle (Ov), forming external ear (Ee). Shallow grooves indicating the beginning of digit formation (D). E15: further projected external ear (Ee), and ear canal covered by the pinna. The peripheral vessels (V) were visible over the body due to little skin pigmentation. E17: longer fore and hind limbs (FL and HL, respectively) with separated digits. PN0: Separated digits with early formation of claws were visible at the ends of the fore and hind limbs (FL and HL, respectively), skin pigmentation, further formation of pigmented optic vesicle (Ov). PN10: the eyes were still covered by a layer of skin (E), deeper grooves were visible between the digits (D). PN15: feeding on hard foods (such as corn) (arrow) and near to weaning. PN20: individuals exhibited completely similar features to neonates, with elongated, well-developed bodies and longer tails (T). Scale bars indicate 5 mm in the upper row and 10 mm in lower row

stage. Tail length in the newborn (23 ± 0.8 mm) was approximately 27% of that in adult length (84.5 ± 1.2 mm), reaching 94.1% in juveniles (80 ± 0.6 mm). Length growth was more rapid prior to weaning (PN35) as compared with weight (Fig. 2) with a 50.7% and 11.9% increase, respectively. After weaning, these rates were inversed but rather similar (77.05% and 84.7%, respectively). Differences in the rates of development between the periods of growth from newborn to juvenile and from juvenile to adult were also observed. Although, about a seven times increase was observed in the rate of weight gain from juvenile to adult (84.7%) compared to the period from newborn to juvenile (11.9%), the rate of growth in the head and body length showed only about a 1.5% increase from juvenile to adult compared to newborn to juvenile (Fig. 2). Length exhibited a different growth pattern (= rate of growth) compared with body weight in the first 20 days, where length rapidly increased but abruptly decreased after this age (Fig. 2 and Table 1). The total length at the age of 20 days was 83.3% (134.2 ± 0.9 mm) of its adult size (162 ± 0.8 mm). Hind foot in newborns (6.8 ± 0.2 mm) was about 33.3% of adult length (21.2 ± 0.5 mm) and grew to 95.2% in juveniles (19.7 ± 0.5 mm). The hind foot grew rapidly during early life reaching its maximum size at 35 days of age. Generally, sexual maturity was not reached at less than 4 months for both males and females. Reproduction in males began at 5 months of age, whereas first pregnancy usually occurred in 6–7-month-old females (also see Kilpatrick 2017). Our observations showed that Goodwin's brush-tailed mice are sexually mature when their tail tuft is at least 6 mm long and the hind foot is at least 21 mm.

At birth, golden hamsters have a body mass of 2.8 ± 0.07 g, a head and body length of 31.8 ± 0.8 mm (Table 1), and eyes that were still covered by a layer of skin (Table 2). Faster development of fore limbs was observed as compared with hind limbs (Fig. 3). The body mass of juveniles at weaning (PN15) was about 24.7% (17.9 ± 0.8 g) of the adult weight with a head and body length of 70.1 ± 0.5 mm (about 46.8% of the adult length) reaching 72.2 ± 0.5 g and 149.6 ± 1.7 mm in adults, respectively. Growth rate of head and body length was rapid (45.6%) both before and after weaning (PN15) as compared with that of weight increase (19.8%). However, no obvious changes were observed in the increasing rate of length in the first two stages of postnatal life (PN0-PN15 and PN15-adult) (see also Table 1 for more details).

We found house mouse newborns body mass to average 2.4 ± 0.08 g at birth with a head and body length of 31.4 ± 1.1 mm (Table 1). Separated digits with early formation of claws were visible at the ends of the fore and hind limbs at this stage (Fig. 4 and Table 2). The body mass of juveniles at weaning (PN16) was 12.7 ± 0.3 g with a head and body length of 64.5 ± 0.9 mm, about 46.1% and 75.2% of the adult weight and length, respectively. In adults, weight averaging was 27.5 ± 0.4 g and length was 85.7 ± 0.9 mm. Similar to golden hamster, growth rate of head and body length was rapid (61.8%) both before and after weaning (PN16) as compared with that of weight showing a 32.4% increase. However, approximately two-fold increases were observed in the growth rates of weight and

head and body length in the second stage of postnatal development (PN16-adult) compared with the rates during the first stage (PN0-PN16) (see Table 1 for more details).

Discussion

The interaction between duration of pregnancy and developmental rate apparently explains the timing of postnatal life history, indicating that developmental rate and timing parameters govern the entire postnatal period (Zelditch et al. 2003a). There have been several studies on postnatal development of rodents especially model organisms such as house mouse and hamster (e.g., Cardini and O'Higgins 2005; Cubo et al. 2006; Fadda and Leirs 2009; Zoccolan et al. 2009). However, only a few studies have focused on postnatal development of brush-tailed mice (Meyer and Malikov 1996; Volf and Volf 2003, Hamidi et al. 2017b, 2018) and the only study on prenatal development of these rodents focused on tooth morphogenesis (Hamidi et al. 2017b).

Herein, we showed that Goodwin's brush-tailed mice are born more developed than either house mice or golden hamsters. With a mean gestation period of 31.5 ± 2.1 days compared with 20.8 ± 0.8 days for house mouse and 15.6 ± 0.8 days for golden hamster, newborns of this species have longer time to develop in utero. However, it still takes longer to reach subsequent postnatal milestones (such as weaning) due to a slower rate of development following birth. The ontogeny of Goodwin's brush-tailed mouse can be divided into five periods with different growth rates: E0-17, E17-PN0, PN0-PN15/PN20, PN15/PN20-PN35 (juvenile), and PN35 to adultness. In the first period, prenatal growth is rapid and in the second period, it is reduced (Fig. 2). After birth, we observed rapid growth in weight and body length up to PN15 and PN20, respectively. However, in the fourth period, growth is slowed down and in the last period, growth almost ceases.

We observed very rapid prenatal development and also early maturity in golden hamster. Regarding size, little differences were observed among the newborns of the three species at birth. Golden hamsters were the largest species examined, whereas Goodwin's brush-tailed mice and house mice were similar in size but smaller than the golden hamster. Weight and head and body length exhibited different growth rate (and pattern) after birth in the three species examined. In Goodwin's brush-tailed mice, the increase in weight was more dynamic than the change in head and body length, up to adultness. In golden hamster, head and body length showed a stable rate of growth before and after weaning (45.3% as the rate of growth from newborn to juvenile vs. 46% as the rate of growth from juvenile to adult), but for body weight, this was slightly greater after weaning (15.6% as the rate of growth from newborn to juvenile vs. 24% as the rate of growth from juvenile to

adult). For house mouse, weight and head and body length growth were both equally dynamic up to adultness. For head and body length, the rate of growth from newborn to juvenile was 48.6% vs. 75% as the rate of growth from juvenile to adult. For body weight, 18.8% was indicated as the rate of growth from newborn to juvenile vs. 46% as the rate of growth from juvenile to adult (Fig. 2, see also Table 1). Moreover, the prenatal morphological growth pattern of the house mouse was different from that of the golden hamster, though their postnatal growth patterns were similar (Figs. 1, 3, and 4).

As found in studies of mammals (O'Higgins et al. 2001; Singleton 2002) and other vertebrates (Monteiro et al. 1997; Zelditch et al. 2003b), even close relatives can differ in their ontogeny. In vertebrates, larger size is associated with slower development, later puberty, and lower fecundity (Angelini and Ghiara 1984; Roff 2002). Nevertheless, despite the small size of Goodwin's brush-tailed mouse, tendencies of *K*-selected reproduction are evident in its slow rates of pre- and postnatal development. One can hypothesize that the reproductive pattern observed in *Calomyscus* is due to their derivation from a lineage with this pattern of reproduction, and the genetic makeup of this group is constrained by its phylogenetic history, the genes and genetic pathways that were present in its ancestors rather than being adaptive, and the results of selection. However, as we will discuss later, genetic variability can be found in the laboratory "bottle-necked" stock of Goodwin's brush-tailed mice that includes more *r*-selected reproductive characteristics. These observations could be used to reject the null hypothesis of phylogenetic constraint. Hence, we hypothesize that an adaptation to a particular environment played a role to thereproductive strategy within the genus *Calomyscus*.

Members of this genus are generally found in stony or rocky habitats. They are also known to nest in the roots and cavities of oak trees. Furthermore, brush-tailed mice are found in desert regions where they occur beneath dwarf palms (Hamidi et al. 2017a; Kilpatrick 2017). The specialization to such environments requires a number of peculiarities, which are, first of all, mouse-like appearance and a comparatively complicating pattern of locomotion. In *Calomyscus*, locomotion pattern is much more complicating than golden hamster and non-rocky (meadow) voles; they can jump and climb and use their long tail as a balance, while meadow short-tail voles move like "quadrupedal pouches" (author's observation). It should be mentioned that mouse-like exterior and complicated locomotion seem likely to be based on more prolonged ontogenesis when comparing the forms, which are characterized by the same kind of reproductive strategy. For example, most of the *r*-strategic plain voles are characterized by more rapid kind of postnatal ontogenesis, than *r*-strategic house mouse (Malikov and Meyer 1990). Therefore, we further hypothesize that in the case of brush-tailed mice, the considerable prolongation of ontogenesis is based on a mouse-like kind of exterior and

complicating pattern of locomotion, on one hand, and K-reproductive strategy on the other hand. According to Pianka (1970), in such situation "…competition is keen and the optimal strategy is to channel all available matter and energy into maintenance and the production of a few extremely fit offspring."

Golden hamster, which is larger than the others in this study, displays a higher tendency to r-kind reproductive strategy. Periodic fluctuations of population density are considered as an indicator of r-strategy (Krebs and Myers 1974). Nevertheless, there is no evidence about its population fluctuations because it has a very restricted range and appears to be threatened in the wild due to extensive pest control methods and perhaps competition for forage with livestock. Golden hamsters in laboratory conditions exhibit r-reproductive strategy (Gattermann et al. 2001). Another indicator can be a tendency to pest activity, which seems to be impossible for small K-strategic mammals.

The adaptive zones (= ecological niches) related to species of the same genus and closely related genera with rather similar mode of existence (e.g., Ciscaucasian hamster, *Mesocricetus raddei* (Nehring, 1894), Turkish hamster, *Mesocricetus brandti* (Nehring, 1898), European hamster, *Cricetus cricetus* (Linnaeus, 1758)) are characterized by the following features in common: seed diet with a small vegetative quota, solitary mode of existence, spatially continuous habitats within dry steppe zones, evident fluctuations of population density and tendency to crop pest activity (except *Mesocricetus raddei*). Moreover, the introduction of the golden hamster into a laboratory condition also shows an evident potency to r-kind of reproduction (Magomedov and Omarov 1995; Surov et al. 2015; Feoktistova et al. 2016). The adaptive zone of the golden hamster is closer to the so-called "perfect ecologic vacuum," which was characterized by Pianka (1970) as "a lack of density effects and competition," where "the optimal strategy is to put all possible matter and energy into reproduction, with the smallest practicable amount into each individual offspring, and to produce as many total progenies as possible."

In the golden hamster, there is a lack of heterochrony between pre- and postnatal development; both of them were characterized by a higher rate, as compared with the house mouse and especially Goodwin's brush-tailed mouse. In the house mouse, there is an evident heterochrony between pre- and postnatal development. The domestic mouse displayed nearly similar patterns of early prenatal growth and development as Goodwin's brush-tailed mouse and similar early postnatal growth (up to the end of second week of life) with both Goodwin's brush-tailed mouse and golden hamster. The house mouse is known to demonstrate the main indicators of r-reproductive strategy, fast postnatal development, early sexual maturation, high fecundity, and, as a result, catastrophic outbreaks of population density (Laurie 1946; Bronson 1979). The benefits of r-reproductive strategy for house mouse may

be substantial, taking into consideration that its infants are at an exceptionally high risk of mortality (Zelditch et al. 2003a), due to nesting in habitats commensal with humans. Although commensal habitats provide benefits like offering potentially rich food resources, but are also characterized by instability in space and time compared with natural and semi-natural (non-commensal) habitats. Breeding and reproductive rate, survival and mortality rates, migration and dispersal, and flexibility in spatial organization are variables which can be used for testing the hypothesis of great mortality of house mice in anthropogenic habitats than in the wild. According to Pocock et al. (2004), "Non-commensal house mice have lower mortality, seasonal breeding, and individuals move more frequently and further than commensal house mice." As a whole, Goodwin's brush-tailed mouse and the house mouse appeared to be rather similar in early morphological development, whereas the golden hamster development was different from these two.

Among these three species, Goodwin's brush-tailed mouse displayed a complex K-reproductive strategy, where late sexual maturation (not earlier than 4 months) is a direct consequence of a slow prenatal and subsequent postnatal development. However, in the laboratory "bottle-necked" stock of Goodwin's brush-tailed mouse, approximately 20% of individuals opened their eyes on the 12th day of life (Meyer and Malikov 1996) and 1 female out of 20 (5%) produced 1 litter per month for half a year, which reveals a cryptic potential of more r-reproductive characteristics in this species. The "bottle-neck" effect is inevitable when only a few parental individuals from natural genetically polymorphic population give an origin to the laboratory stock. Such stock inevitably has a much reduced genetic variation, that can "open the road to phenotype" to some characters, which are not revealed in enough polymorphic populations. In the case of brush-tailed mice, which are K-strategic in the wild or in nature, in their laboratory stock, there were some characters of r-reproductive strategy, as mentioned above.

All the reproductive and developmental elements of the golden hamster are r-strategic kind, while some elements of r-strategic *Mus musculus* development are similar to the K-strategic *Calomyscus*. In the golden hamster, pre- and postnatal development, including sexual maturation, is comparatively rapid. We propose that this species is a good example of a basic evolutionary shift towards r-reproductive strategy, at both pre- and postnatal levels. With regard to r-reproductive strategy of the house mouse, it presumably was not completely "turned on" at the level of prenatal development. In the house mouse, pre- and postnatal rates of development are different, demonstrating heterochrony in its development. As a result, the house mouse combines comparatively slow episodes of prenatal development with rapid postnatal development and r-kind of reproduction (Rugh 1968; Kotenkova and Priluzskaya 1994).

Previous studies (Malikov and Meyer 1990; Meyer and Malikov 1996) have revealed several facts on fecundity and postnatal ontogenesis of voles (Cricetidae: Arvicolinae) with *r*- or *K*-reproductive tendencies including data on intraspecific variants and extremes of fecundity (maximal litter size and minimal age of a pregnant female) in laboratory stocks of voles species European snow vole, *Chionomys nivalis* (Martins, 1842), Caucasian snow vole, *C. gud* (Satunin, 1909), and Robert's snow vole, *C. roberti* (Thomas, 1906) which could serve as potentially raw materials for evolutionary shifts of reproductive strategy. Among voles, the stenobiotic species, which normally show the *K*-reproductive strategy, are strictly associated with fragmentary habitats of a particular kind. They are, for example, such alpine species of the genus *Chionomys*, as European snow vole and Caucasian snow vole, which in contrast to lowland meadow or steppe vole species of comparatively continuous habitats, live only in rocky areas. The laboratory stocks of those stenobiotic alpine species of the genus *Chionomys* displayed comparatively slower postnatal development (eyes opening on 11th–13th day, and the first pregnancy no earlier than the third month) than the lowland ones, but the same duration of pregnancy (20 days) (Malikov and Meyer 1990). Therefore, they presumably have similar patterns of prenatal development with species living in the lowlands. The laboratory stocks of lowland non-stenobiotic vole species, which show evident fluctuations of population density in nature, were characterized by a typical *r*-kind of reproduction (capacity of producing a litter per 20 days for several months) and a high rate of postnatal development (eyes opening on 9th–10th day, and the first pregnancy mainly in 3-month-old females) (Malikov and Meyer 1990). In the stenobiotic European snow vole (*Chionomys nivalis*), approximately 25% of females in their "bottle-necked" laboratory stock demonstrated a tendency to more or less *r*-reproduction (Malikov and Meyer 1990). In addition to these examples of reproductive flexibility, it has been reported that such typically *r*-strategic voles such as the bank vole *Myodes glareolus* (Schreber, 1780) can produce either *r*- or *K*-reproductive cohorts dependent on environmental conditions (Olenev 2002).

Conclusion

According to Creighton and Strauss (1986), differences in the length of gestation, postnatal growth rate, and duration of growth might reflect relative selection on life history traits or may represent differences due to phylogenetic history. The results of our study showed possibility of both scenarios. In the golden hamster, and likely all true hamsters, rapid growth and development in both pre- and postnatal stages are hypothesized to be the results of their quite ancient occupation of an adaptive zone, where the tendency to *r*-kind of reproduction was the most optimal. For house mouse, considering the high risk of mortality and other topics mentioned earlier, heterochrony observed between pre- and postnatal development as well as *r*-reproductive strategy provides lots of benefits. In contrast, long-term development and tendency to *K*-reproductive strategy in brush-tailed mice probably have resulted in better survival due to living in discontinuous habitats with usually difficult environmental conditions and limited food resources which can threaten them. In addition, *r*- or *K*-kind of fecundity can be switched on epigenetically by different environmental conditions, as was shown by Olenev (2002).

Developmental patterns and their phenotypic endpoints reflect the ecological history of the taxa studied. Now, while looking back to the basic "*Evo-Devo*" approach, according to which the evolutionary changes mainly do not happen in adults, being the results of shifts in ontogenetic pathways, it is getting clear that the strategy of reproduction is characterized by a high flexibility of maintenance, with the following approaches: (1) developmental self-consistence, where reproduction strategy is directly determined by pre- and postnatal development of either slow (*K*) (in Goodwin's brush-tailed mouse) or fast (*r*) (in golden hamster) kind; (2) heterochrony, where some episodes of prenatal development are hypothesized to be ontogenetic rudiments of historically reproductive strategy, whereas an alternative strategy is hypothesized to result primarily from postnatal adaptations (such as in *Mus* and *Chionomys*); and finally (3) epigenetic switching on the reproduction of either *r*- or *K*-kind (*Myodes* and obviously most of the non-stenobiotic voles and lemmings) (Olenev 2002).

In summary, our results demonstrate that despite external similarities at birth between Goodwin's brush-tailed mouse, golden hamster, and house mouse, they manifest some evident developmental differences at pre- and postnatal periods. Moreover, we hypothesize that prenatal characters may be under greater phylogenetic constraints, whereas postnatal development appears to be amenable to selection in the short term leading to adaptation. These differences might provide clues to evolutionary modeling the *r*- or *K*-reproduction maintenance. Such speculations, however, awaits further experimental investigations.

Comparison of the developmental process and growth data of different species of brush-tailed mice is suggested for a better inference of speciation and habitat specialization in this group. Cladistics analyses on various morphological and morphometric characters during the pre- and postnatal development of different species of Calomyscidae, identifying intraspecific polymorphisms as well as synapomorphies for the family, comprehensive evolutionary comparative studies on different characters of this basal group, and other muroid rodents, and also extracting plesiomorphic characters will be informative for exact determination of evolutionary pathway of these rodents, which are an early diverging clade of the Eumuroida, based on *Evo-Devo* approach.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of Ferdowsi University of Mashhad.

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