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High inter-individual variation in the gestation length of the hedgehog tenrec, *Echinops telfairi* (Afrotheria)

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Abstract

The gestation length (GL) of Tenrecs (Tenrecinae, Afrotheria) is still uncertain. This lack of knowledge also applies to the lesser hedgehog tenrec, *Echinops telfairi*, the species most commonly bred and maintained in captivity. The animals used in this study were held under controlled conditions (light, temperature and humidity). In order to determine the GL, groups of female tenrecs were subjected to various mating procedures followed by isolation periods of different lengths. A total of $n = 249$ pregnancies were analysed and the number of offspring per litter was 3.29 ± 0.09. The length of gestation could be determined in $n = 199$ pregnancies and a mean GL of 67.53 ± 0.36 days was calculated. Initial attempts with isolation periods of less than 16 days did not allow to accurately define the GL. Experiments with longer isolation periods and females subjected to only one mating procedure ($n = 10$) revealed a variation in the GLs of 57–79 days. However, in one female a GL of only 50 days was also observed indicating an even greater range in GL variation. There was a statistically significant tendency for shorter GLs in the animals that conceived later in the mating season, but no statistical evidence was found that age, parity or litter size played an essential role in determining the GL. In conclusion, an unexpected high variability in gestation length in *E. telfairi* was demonstrated although the study animals were kept under controlled environmental conditions. The factors and mechanisms regulating this high intra-species variability in gestation length need further investigations.

Keywords: Pregnancy length; Reproductive delay; Torpor; Insectivore

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1. Introduction

The lesser (pigmy) hedgehog tenrec (*Echinops telfairi*) is kept well in captivity; it is a seasonal breeder delivering between 1 and 10 young (average three to five) once a year (Honegger and Noth, 1966; Eisenberg and Gould, 1967; Godfrey and Oliver, 1978; Poduschka, 1996; Künzle, 1998). Until recently the Madagascan tenrecs were classified with insectivores, but genetic data suggest they have closer affinities with the newly recognized superorder Afrotheria (Robinson and Seiffert, 2004; Nishihara et al., 2005). This taxon includes elephants, hyraxes, sea cows, aardvarks, golden moles, tenrecs, and elephant shrews. Within the Afrotheria the order Afrosoricida includes the family Tenrecidae with about 30 different species.

The tenrecinae have attracted reproductive scientists for decades (Grosser, 1928; Strauss, 1943; Nicoll and Racey, 1985; Thompson, 1992; Poppitt et al., 1994; Stephenson and Racey, 1995; Carter et al., 2005; Enders et al., 2005). Data on their gestation length (40–70 days) and litter size (1–32 young) have been used in various life history studies (Frazer and Huggett, 1974; Eisenberg, 1981; Millar, 1981; Stearns, 1983; Symonds, 2005; Johnson et al., 2001; Langer, 2002). However, the precise gestation length of *E. telfairi* is unknown. The contradictory perceptions regarding its gestation length are included in two recent reference books indicating either 42–49 days (Nowak, 1999) or 60–68 days (Garbutt, 1999). Obviously, such data are difficult to use in search for life history traits, and they scarcely allow a characterization of particular developmental stages and possible delays (Vogel, 1981; Mead, 1993; Renfree and Shaw, 2000). Thus the aim of the present study was to define more accurately the gestation length (GL) and its variation in *E. telfairi* (Et).

2. Materials and methods

2.1. Animals and environment

The lesser hedgehog tenrecs used in this study belonged to a colony of about 500 animals kept in Munich. This colony was founded between 1979 and 1982 with animals received from different sources including four Echinops from Madagascar. All animals used for breeding purposes were marked and recorded, and attention was given not to mate animals with identical parents and grandparents (Künzle, 1998).

Almost all tenrecs analysed in this study were held in the same room. In order to simulate the annual activity cycle in their native habitat in south-western Madagascar (high aridity, relatively low temperature, scarcity of food during the topor phase) the tenrecs were exposed to reverse schedules of light (13 h from end of March until July), temperature (24–26 °C) and humidity (60–80%). Food (canned cat food, dog sausages, dry food, occasionally bananas) was given in the early morning according to a schedule described previously (Künzle, 1998). Water was always present in the cage and renewed 5 times a week.

Usually, two to five animals were housed in an aluminium cage (45 cm × 60 cm × 34 cm) with dust-free sawdust used as litter. The walls (in part also the ceiling) were made of metal plates with regularly punched holes allowing the animals to climb. Each cage contained at least one wooden nestbox consisting of two rooms covered with a lid which could be lifted easily. Within the main room of this nestbox (10 cm × 10 cm) up to five animals might be packed tightly together, even in the cases where an additional empty box was present.

2.2. Mating procedures and mating sessions

The study animals awoke from torpor between mid-February and mid-March. In view of the facts that Echinops give birth only once a year and the final litter size is relatively small (3–4 young) we previously employed a mating procedure consisting of a regular exchange of females every 8–10 days without any separation from the male. This practice did not identify the exact gestation length and therefore was changed for the present study. The reproductive management applied in the years 2002, 2003, 2004 and 2005 included the separation of males and females at the beginning or the end of the topor phase, and the separation of males and females between subsequent pairings, termed mating sessions (MS; Table 1). Up to three MS per year were employed and numbered with letters a, b and c. For the MS usually experienced (proven breeders) and inexperienced males for a particular female were used in an alternating way. Between the MS the females were separated from the males and were kept in groups of 3–5 animals per cage.

Because the duration and/or the number of copulations necessary for a conception were unknown, various mating procedures (MP, numbered with letters H–R) were tested. The schedules of the MPs varied with regard to the number, the interval between, and the duration of MS (Table 1). In addition, some MS were interrupted with breaks.

In the year 2002 males and females were separated at the end of the torpor phase and the first MS (MS-a) usually consisted of two sub-sessions. In MP-H the MS-a consisted of an initial 4–6 h contact between male and female, their separation for 42 h and a second contact for 24–26 h. In MP-I the females during MS-a were placed with a male for 19 and 48 h, respectively, with an intervening separation period of 27 h. In MP-J one female (Et1482) was placed with a male and surveyed continuously; Et1482 was mated only once (von Schweinitz and Thomsen, 2003). The other three females were mated for 2 d with no subdivision of MS-a.

MPs in the year 2003 were hampered by construction work and a dislocation of the animals into another room at the end of their torpor phase. Owing to this dislocation during the mating and gestation period, only two breeding groups were available. The MPs had uninterrupted MS-a, longer intervening separation periods between the pairings and after the MS-c males and females were separated for at least 1 week.

In 2004 the majority of females were kept separated from the males during the entire torpor phase. Mating sessions consistently lasted 1 day and the intervening separation periods were at least 3 weeks. In MP-M no MS-c was included and nine pregnant females of this group were mated only once.

In 2005 the females were kept isolated from the males for 4–6 weeks prior to MS-a; only two MS were applied lasting consistently 1 day and the intervening separation period was at least 4 weeks.

2.3. Post-mating management and birth

The females considered pregnant were separated from their female cage mates and put into a separate cage, for reasons of limited space usually together with a male. The males did not appear to disturb the females (or later their young) provided an additional nestbox was in the cage. The females were checked for birth every day once in the morning, i.e. the females which had delivered and eaten their offspring immediately afterwards, were not recorded in this study.

Table 1
Schedule of mating procedures and mating sessions

Mating procedure	Start of MS-a	Duration of MS-a males and females were (n = days)		Start of MS-b	Duration of MS-a males and females were (n = days)		Start of MS-c	Duration of MS-a males and females were (n = days)	
		Together	Separated		Together	Separated		Together	Separated
MP-H	02 April 2002	1 + 1	15	20 April 2002	3	15	08 May 2002	Continuously	
MP-I	08 April 2002	1 + 2	12	24 April 2002	2	14	10 May 2002	Continuously	
MP-J[a]	22 April 2002	2	12	06 May 2002	2	16	24 May 2002	Continuously	
MP-K	31 March 2003	2	20	22 April 2003	1	21	14 May 2003	1	>7
MP-L	03 April 2003	1	18–24	22 April–28 April 2003	1	21	14 May 2003–20 May 2003	1	>7
MP-M	02 April or 04 April 2004	1	23–38	26 April–12 May 2004	1	Continuously			
MP-M[a]	02 April or 04 April 2004	1	Continuously						
MP-N	24 March 2004	1	26	20 April 2004	1	21	21 May 2004	1	>9[b]
MP-O	29 March 2004	1	26	25 April 2004	1	21	17 May 2004	1	Continuously
MP-P	27 April 2004	1	21	19 May 2004	1	>14			
MP-Q	05 April 2005	1	28	03 May 2005	1	>16			
MP-R	07 April 2005	1	33	10 May 2005	1	>21			

[a] One and nine pregnant females of groups MP-J and MP-M, respectively, were mated only once.
[b] One pregnant female conceived in MS-c and was separated for >45 days.

2.4. Data analysis

A total of 249 pregnancies were observed, however, the day of conception and thus the gestation length could not be determined with 100% certainty in all cases. A total of $n = 199$ gestations were further analysed. Results are presented as mean ± S.E.M. In the cases were MS lasted for more than 1 day, the first day of the MS was used for GL calculation.

3. Results

Results including the MS and MP are presented in Table 2. Details on the age, the number of parturitions per female and litter size are shown in Fig. 1. Animals started breeding at the age of 1 year and the oldest female that gave birth in this study was 7 years. The number of offspring per litter was 3.29 ± 0.09, and thus almost identical to the results reported with the previously applied forced mating procedure (Künzle, 1998).

Days of conception and parturitions were grouped in weekly intervals and aligned to the time of the year; most conceptions occurred in April, whereas birthing mainly took place in June (Fig. 2). The pregnancy rate in this study was about 50%. It is not possible to present absolute values for all experimental groups, as animals which died during the course of the study might have included some overlooked pregnancies. In addition, some animals might have eaten their offspring unnoticed after parturition. Examples of pregnancy rates were calculated for MP-H, I, M and N; these were 54%, 30%, 54% and 45%, respectively.

The most accurate information regarding the GL was obtained from the females which were separated from the males for at least 20 days and which conceived in MS-a ($n = 138$). The GL varied between 57 and 79 days, respectively (Table 1, Fig. 3). However, in the MP-Q group one animal with a gestation length of only 50 days was observed, indicating an even higher GL variation than the 57–79 days mentioned above. There were examples in which the GL could not be determined with absolute certainty, e.g. the GL in some females was either between 46 and 56 days, or 75–79 days, respectively. In these situations we considered the longer GL as the more

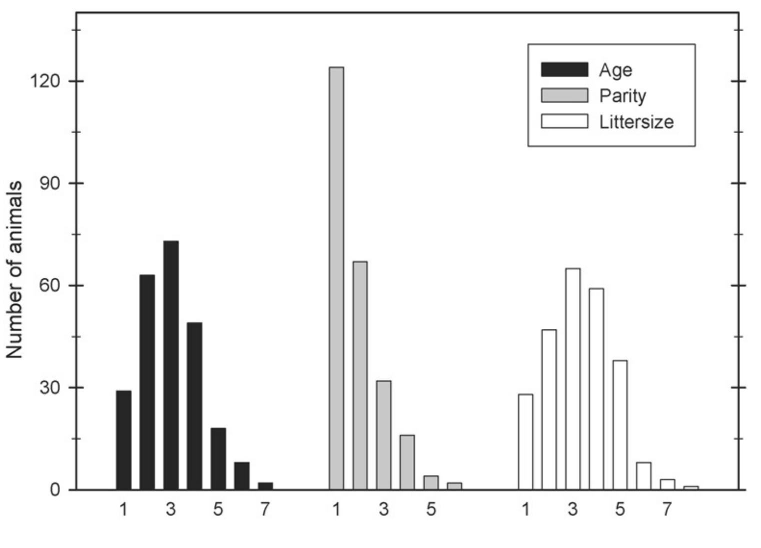

Fig. 1. Age, number of parturitions, and litter size of *Echinops telfairi* females analysed in this study.

Table 2
Variations in the gestation length of *Echinops telfairi* after various mating procedures and mating sessions

Mating procedure	Number of females that gave birth	Parturitions occurred between		Number of GL that could be calculated	Variation in GL (days)	Number of conceptions assigned to mating session:		
						MS-a	MS-b	MS-c
MP-H	58	26 May 2002	11 July 2002	28	63–72	17	11	0
MP-I	11	20 June 2002	03 July 2002	4	67–70	0	4	0
MP-J	4	28 June 2002	11 July 2002	3	65–68	3	0	0
MP-K	23	27 May 2003	03 July 2003	20	57–72	17	3	0
MP-L	15	03 June 2003	04 July 2003	15	60–73	8	7	0
MP-M	25	01 June 2004	24 July 2004	23	57–79	17	6	0
MP-M	9	03 June 2004	22 June 2004	9	62–79	9	0	0
MP-N	35	26 May 2004	27 July 2004	33	60–78	20	12	1
MP-O	13	27 May 2004	04 July 2004	11	59–76	7	4	0
MP-P	8	21 June 2004	11 July 2004	7	57–75	7	0	0
MP-Q	37	02 June 2005	14 July 2005	35	(50) 57–78	28	7	0
MP-R	11	07 June 2005	19 July 2005	11	58–76	5	6	0
Total	249			199 (100%)		138 (69.3%)	60 (30.2%)	1 (0.5%)

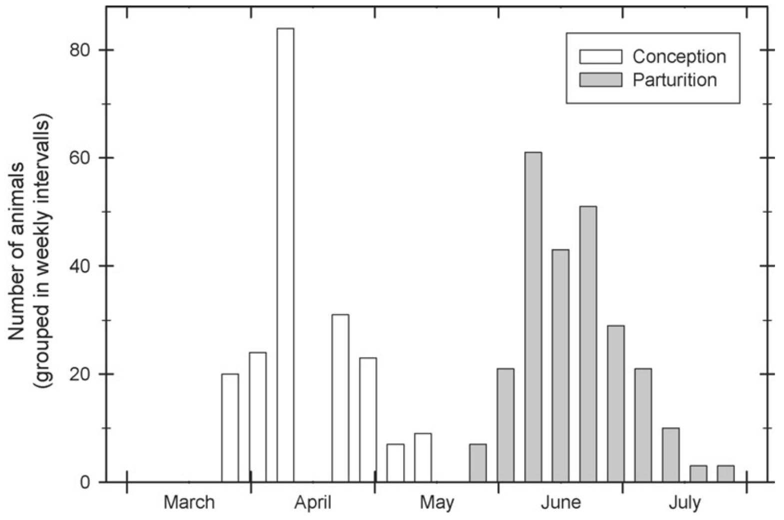

Fig. 2. Conceptions and parturitions in *E. telfairi* grouped in weekly intervals and aligned to the time of the year. Bars for the generation of conceptions included $n = 199$ pregnancies; bars for parturitions included all birth ($n = 249$) analysed in this study.

likely length because in 10 animals mated only once (nine animals from MP-M and one animal from MP-J) the GLs were between 62 and 79 days. The questionable values of GL below 52 days in length were not included in our calculation on the average GL. Likewise results of certain individuals which had GL of 82 or 53 days or 80–81 versus 54–55 days were not included in the calculation.

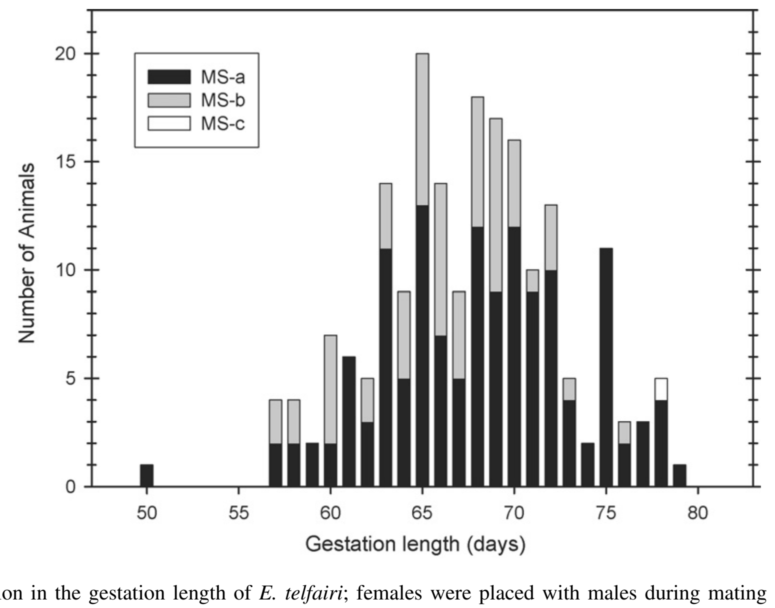

Fig. 3. Variation in the gestation length of *E. telfairi*; females were placed with males during mating sessions MS-a ($n = 138$), MS-b ($n = 60$) and MS-c ($n = 1$). The length of separation between the MS varied according to the protocol of the mating procedures (details are listed in Table 1).

Results on the GL are shown in Fig. 3. We finally identified two groups, one for which the GL was determined as very likely or likely ($n = 199$), and a second group for which GL could not be determined ($n = 50$). Results from the second group were not further analysed. The mean values for the GL classified as very likely or likely were 67.14 ± 0.43, and 68.25 ± 0.67 days, respectively, but the difference was statistically not significant. Therefore, results of both subsets were combined and a mean ± S.E.M. of 67.53 ± 0.36 days was calculated.

The GL columns were subdivided with regard to mating sessions a–c (Fig. 3); the GL in the MS-a ($n = 138$) and MS-b ($n = 60$) groups were 68.12 ± 0.45 and 66.0 ± 0.53 days, respectively. The difference between these groups was statistically significant ($p < 0.01$; Mann–Whitney Rank Sum Test). While the MS did seem to influence the GL (the only definite MS-c case, however, showed a GL of 78 days), the GL was independent from the mating procedures and there was also no statistically significant correlation between age or litter size and GL. Furthermore there was no statistically significant correlation between parity or age, and litter size.

We compared the intra-individual GL over the study years. Among the 201 parturitions analysed between 2002 and 2004, 23 females with two parturitions and eight females with three parturitions were included. We assumed high, moderate and low coincidences when the individual GLs varied within 4 days, between 5 and 7 days or over 8 days, respectively. Among the 31 investigated cases there were 10, 13 and 8 cases with high, moderate and low coincidence, respectively. In the three mentioned groups two, three and four females had three parturitions each.

4. Discussion

This study concerns the re-determination of the Echinops' gestation length and the demonstration of a high variability despite the fact that the animals have been held under controlled and very similar environmental conditions. It is striking in this instance that the Tenrecidae have much longer gestation lengths than would be expected for their body mass (Symonds, 1999). The average GL of 67.5 days corresponds to the higher value of the original reports by Eisenberg and Gould (1967), Mallinson (1968) and Poduschka (1996) who suggested a gestation length between 62 and 68 days. The data are also compatible with the findings of Godfrey and Oliver (1978), who described possible GLs of 78, 54, 49, 42 days and 67, 61, 59, 56, 54 and 51 days, in two animals. However, these authors suggested a GL around 50 days or shorter, but it is possible that in their study the high room temperature of 27–30 °C has shortened the GL. Nevertheless, according to our current results the mating intervals used by Godfrey and Oliver (1978) were too short for an evaluation of the Echinops' GL and a length of more than 70 days cannot be excluded a priori. This is also true for our previous misinterpretation (Künzle, 1998).

A true variation in the length of the Echinops' gestation has been noted before (Eisenberg, 1975; see also Stephenson and Racey, 1993) although not to the extent shown in the present study. An indication to an even greater extent than from 57 to 79 days is gained from individuals in this study with GLs of 50 days or animals with either 54 or 80 days, 55 or 81 days and 53 or 82 days. Aware of these data some GLs judged as between 76 and 78 days may, therefore, also be interpreted as being between 52 and 55 days. Whatever the extremes of the Echinops' GL are the core period of 57–79 days results in an inter-individual variation index of 32.4% (extent of variation divided by the average GL), a very high value in comparison to other species. The great majority of placental mammals have values below 6% (Eisenberg, 1981; Kiltie, 1982; Sandell, 1990). A variation index above 20% is only seen in few species, e.g. the striped skunk (26%; Wade-Smith et al., 1980), some minks (up to 75%; Mead, 1993), a few bats (Rasweiler and

Badwaik, 1997; Heideman and Powell, 1998) and possibly the large eared tenrec (Stephenson and Racey, 1993).

The major adaptive value of intra-specific variation in GL is thought to allow mating to occur and young to be born at times most favorable for the species. Usually, different gestation lengths are used to modify the fluctuations in the time of mating and to give birth within a circumscribed period under optimal conditions such as the availability of food and best climatic circumstances (Rutberg, 1987; Berger, 1992; Mead, 1993; Renfree and Shaw, 2000; Thom et al., 2004). In cases of birth synchrony the anti-predator benefit also plays an important role. Major factors controlling the timing of these events are photoperiod, odour, ambient temperature and humidity (Bronson, 1985; Ims, 1990; Lopes et al., 2004). Obviously, such reasoning cannot explain the variations seen in our study population, as their mating was timed and parturitions were asynchronously distributed. In addition, the animals were housed under very similar conditions, particularly with regard to light, humidity, temperature and food availability. Also litter size, age and parity of the females did not appear to play a significant role in determining gestation length. In addition, a lactational delay as seen in postpartum pregnancies of various mammals (Vogel, 1981; Mead, 1993) cannot explain the variable gestation lengths in Echinops delivering only once a year.

Also the variable presence of males during late gestation is not considered crucial since pregnant females entirely isolated from a male showed similarly high variations in their GL as the females sharing their cage with a male. Nevertheless, social cues through variable numbers of cohabitant females between the mating sessions and the occasional occurrence of vibrations from nearby construction work cannot be ignored as possibly affecting the GL. Stress in the short-tailed fruit bat was ascribed as important factor for an inter-individual variation in GL (Rasweiler and Badwaik, 1997). This very high variation, however, occurred in wild populations during their first year in captivity, while most bats born and mated in captivity had quite circumscribed gestation periods between 113 and 119 days.

Another possible explanation for the observed variations may be differences in metabolism due to torpor. Comparable to the short torpor periods in some bats (Audet and Fenton, 1988; Bernard and Cumming, 1997; Racey and Entwistle, 2000) active Echinops also show daily torpid phases (Scholl, 1974; Thompson, 1992). On the other hand, during pregnancy the usually heterothermic Echinops become homeothermic and substantially increase their extremely low resting metabolic rate (Poppitt et al., 1994; Stephenson and Racey, 1995). Thus, there is no experimental evidence yet for torpor phases influencing metabolism and growth during pregnancy (Thompson, 1992; Poppitt et al., 1994), and certainly not to the extent of the variations demonstrated in this study.

Alternatively, short torpor periods may influence ovulation and fertilization (Crichton, 2000; Zhao and Dean, 2002). It is worth to mention in this respect, that the tenrec is a species with a thin, if any tunica albuginea and follicules without antra (Enders et al., 2005), and the possibility of intra-follicular fertilization was suggested (Nicoll and Racey, 1985). In addition ovulation is thought to be induced (Eisenberg, 1975). It is also known that the endphase and the awakening from the true torpor period does vary considerably between individuals (Godfrey and Oliver, 1978) and may additionally influence ovulation and/or conception. However, if the high inter-individual variation relates to the torpor endphase, a more significant difference in the distribution of GL following the first (a) and the subsequent (b and c) mating sessions would have been expected. Also striking is the relatively high overlap of annual GLs in individual animals, which supports the notion that endogenous factors might be involved.

In conclusion, a high variability in gestation length in *E. telfairi* was demonstrated although the study animals were kept under controlled environmental conditions. We do not know yet the factors leading to this variability not to mention the particular mechanisms (differential viability/storage of sperm, diapause, discontinuous growth) and reproductive stages involved (fertilization/ovulation, pre- or postimplantational period). Further investigations involving, i.e. endocrine studies are needed to answer these questions. In this respect the *Echinops* could serve as a model species for other tenrecs, in which similar variations in GL might occur (Eisenberg, 1975; Stephenson and Racey, 1993). Understanding their reproduction would possibly also shed light on other species of Afrosoricidae and thus be of great interest from an evolutionary point of view.

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