Reproductive Biology of the Large-Eared Tenrec, *Geogale aurita* (Insectivora : Tenrecidae)

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Summary. – The reproductive biology of the large-eared tenrec, *Geogale aurita*, was studied in captivity in Madagascar. Four out of ten breeding females exhibited postpartum oestrus, the first time this phenomenon has been recorded within the Tenrecidae. Gestation length was variable, possibly due to some pregnant females entering torpor. Mean gestation length was 57 days confirming that all tenrecs have a uniformly slow foetal development rate. Litter size ranged from 2-5 neonates with a mean of 3,9. Intraspecific variation in neonate mass and growth rate was correlated with litter size, but age at eye-opening and age at weaning did not vary significantly between litters. Post-natal development rates in *G aurita* were the same as in other oryzorictine tenrecsbut slower than in similar-sized shrews. It is concluded that development rates in the Tenrecidae are determined by phylogenetic constraints but postpartum oestrus in *G. aurita* may represent an adaptation to an unpredictable environment.

Résumé. – La biologie de la reproduction de *Geogale aurita* a été étudiée en captivité à Madagascar. Quatre femelles sur dix ont montré un « oestrus postpartum », phénomène noté pour la première fois chez les Tenrecidae. La durée de la gestion est variable, peut-être du fait de l'entrée en torpeur chez certaines femelles gestantes. La durée moyenne de gestation est de 57 jours, ce qui confirme que les Tenrecidés ont un développement fœtal lent. La taille de la portée est de 2 à 5 jeunes avec une moyenne de 3,9. La variation du poids des jeunes et leur taux de croissance sont corrélés à la taille de la portée mais l'âge de l'ouverture des yeux et celui du sevrage ne varient pas entre les portées. La vitesse du développement post-natal de *G. aurita* est comparable à celle d'autres Tenrecidae de la sous-famille des Oryzorictinae, mais elle est moins rapide que chez les musaraignes. On conclut que la vitesse du développement chez les Tenrecidae est déterminée par des contraintes phylogénétiques ; mais l'« oestrus postpartum » chez *G. aurita* peut représenter une adaptation à un environnement imprévisible.

INTRODUCTION

The family Tenrecidae (Mammalia : Insectivora) is an ancient lineage of eutherian mammals endemic to the Indian Ocean island of Madagascar (Eisenberg and Gould 1970). The family comprises two subfamilies (Tenrecinae and Oryzorictinae) with 24

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species in eight genera (Genest and Petter 1974; Nicoll and Rathbun 1990). The reproductive biology of the subfamily Tenrecinae is relatively well studied (e.g. Gould and Eisenberg 1966; Eisenberg and Gould 1967; Riordan 1972; Poduschka 1974; Godfrey and Oliver 1978; Nicoll and Racey 1985) but the only data available on reproduction in the Oryzorictinae arises from two species of *Microgale* kept in captivity in the USA (e.g. Eisenberg and Gould 1970; Eisenberg and Maliniak 1974; Eisenberg 1975).

Geogale aurita is a small, terrestrial tenrec of the subfamily Oryzorictinae. Although its precise distribution limits are unknown, it appears to be found in the west and south-west of Madagascar, and is particularly abundant in the reserve of Beza Mahafaly (Nicoll and Rathbun 1990). There is only one documented record of *G. aurita* having been kept in captivity. A small population of 1-6 individuals was kept in the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar, between 1985 and 1987 (Nicoll and Rathbun 1990; F. Rakotondraparany, pers. comm.). A female gave birth to one offspring but this subsequently died (Nicoll and Rathbun 1990). There is no other information available on reproduction in this species.

As part of a wider study of the Tenrecidae (Stephenson 1991), a colony of *G. aurita* was collected from Beza Mahafaly reserve and kept at Parc Tsimbazaza, Antananarivo. This paper documents for the first time the reproductive biology and growth of *G. aurita* in captivity.

MATERIAL AND METHODS

Capture and maintenance

A total of 9 male and 13 female *G. aurita* were collected from around Parcel 1 of Réserve Spéciale Beza Mahafaly, Tulear province, south-west Madagascar, during July 1988 and June 1989. The animals were discovered in crevices in decomposing logs on the forest floor. The body mass of captured animals ranged from 5-8.5 g (mean = 6.6 g ± 0.8 SE). Captured animals were fed on termites found co-existing in the rotting wood until they were transported to the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo. At Parc Tsimbazaza, *G. aurita* were housed in glass aquaria (22 × 52 cm, 22 cm deep) and maintained at normal outdoor ambient temperatures (July 1988-April 1990 : range 6.3 - 30.2 °C, mean 19.3 °C). Sunlight was permitted to enter the holding room to provide a natural light cycle. Wood shavings were provided as bedding and pieces of bark and cardboard tubing were used as nests. A diet of orthopteran insects was occasionally supplemented with termites. Water was provided *ad libitum*.

Reproduction

Individuals were held in mixed sex groupings until mid-September when pairs were established. Males were left with females until the morning after parturition.

The captive colony was observed regulary to ascertain dates of copulation and parturition. If a female was not paired at parturition, minimum gestation length was estimated from the date the female was last in the presence of a male. Body mass and head and body length were recorded for each neonate once per week on average to determine mean growth rates over the first 35 days after parturition. To prevent the potential problem of females rejecting newborn litters that had been handeld, the neonates of only five litters were weighed and measured on the day of parturition. Mean age at eye-opening was taken as the mid-point between the time from parturition that all neonates in a litter had eyes closed to the time when all had eyes open. Lactation length was taken as the time from parturition until neonates were feeding on solids and suckling only occasionally.

RESULTS

Copulation and parturition

The first recorded copulation of *G. aurita* was on 15 October in the first year, though the earliest conception date (estimated from average gestation length) was 28 September. Copulation in *G. aurita* was associated with a coital lock, the male being held for up to 21 minutes.

TABLE 1. – Determination of gestation length in *Geogale aurita.* For Female 2 and Female 4, date of conception is an estimate based on the date they were last paired with a male.

Individual	Body mass (g)	Litter size	Date of conception	Date of parturition	Gestation length (days)
Female 2	6.8	2	23-09-88?	25-11-88	≥62
Female 4	8.0	3	23-09-88?	02-12-88	≥69
Female 1	7.5	4	24-11-88	22-01-89	59
Female 3	6.8	3	02-12-88	29-01-89	58
Female 8	7.1	5	03-02-90	29-03-90	54
MEAN	7.2	3.4			c.60

During the two years of study, ten female *G. aurita* bred in captivity. Births were recorded in the austral summer between late November and late March. Four females conceived a second litter at postpartum oestrus so that, whilst suckling the first litter, they were concurrently pregnant with a second litter. This is the first time that postpartum oestrus has been documented in the Tenrecidae.

Growth and development of neonates

Litter size ranged from two to five neonates with a mean of 3.9 ± 0.3 (SE). Offspring were highly altricial, born naked with both the auditory meatus and eyes closed. Mean neonate mass in a litter of three was 0.83 g, whereas neonates from litters of five averaged 0.63 g. These data suggest that neonates from small litters are heavier at birth than neonates from large litters. Mean neonate mass within the five litters weighed on the day of parturition was 0.70 ± 0.05 (SE) g. This gives a mean specific foetal growth rate (Frazer and Hugget 1974) of 0.02 $g^{0.33}.d^{-1}$.

Growth rates of sucklings were correlated with litter size whether measured as increase in body mass (least squares regression : r^2 0.522, $p < 0.05$) or increase in head and body length (r^2 0.644, $p < 0.05$). In each case, sucklings in smaller litters had faster

TABLE 2. – Mean growth rates from parturition to weaning in *G. aurita* sucklings from different litter sizes. Number of litters from which growth rate calculated in parentheses. Adequate growth data were not available for litters containing four sucklings.

Litter size at parturition	**Mean suckling growth rate**	
	$g.d^{-1}$	**$mm.d^{-1}$**
2	0.082 (2)	1.0 (1)
3	0.065 (3)	0.8 (3)
4	-	-
5	0.048 (6)	0.7 (5)

mean growth rates (Table 2; Fig. 1*a*). Mean age at eye-opening was relatively constant and showed no correlation with litter size (r^2 0.118, $p > 0.05$). The longest times to eye-opening occurred in the litters of Females 1 and 6 (Fig. 1*b*), which were the first individuals to give birth in the first and second breeding season, respectively.

Weaning

Age at weaning was often difficult to determine since neonates showed an interest in solid foods before becoming completely independent of the mother. In addition, many attempted to suckle long after weaning. However, young were not generally independent of the female until 5 weeks.

A summary of the reproductive parameters determined for *G. aurita* is presented in Table 3.

DISCUSSION

Copulation

The prolonged copulation witnessed for *G. aurita* (up to 21 minutes) is not unusual in the tenrecs. Eisenberg (1975) notes that Tenrecidae copulate for long periods with mounts ranging from 7 1/2 minutes in *Microgale dobsoni* to more than 28 minutes in *Setifer setosus*.

Postpartum oestrus

During a study of *Tenrec ecaudatus*, a captive female gave birth twice within 25 days and this was seen as evidence of postpartum oestrus (Andriatsarafara 1981). However, the failure of the first born neonates to survive parturition and the very short period (less than half normal gestation length) before the second births suggests that

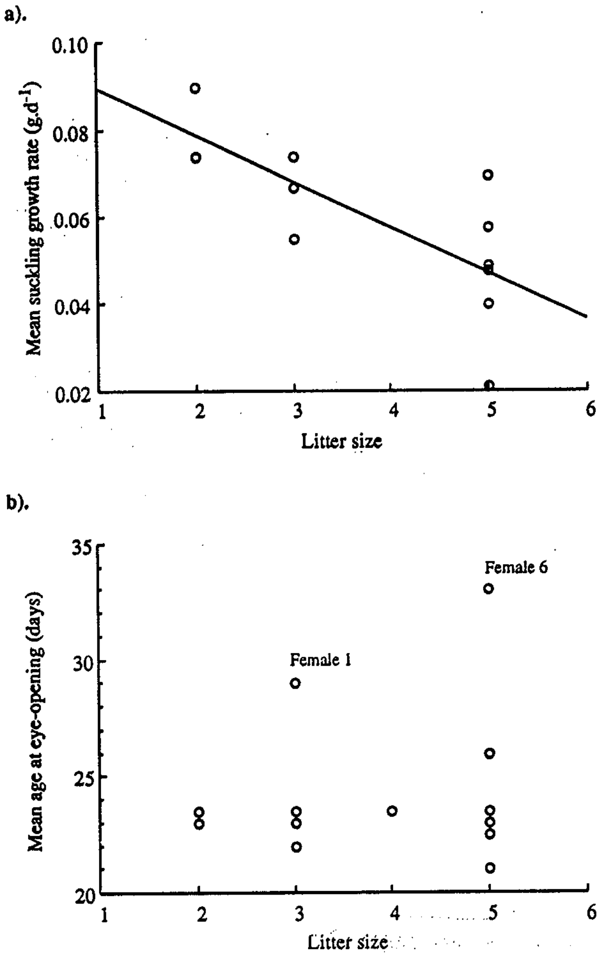

Fig. 1. – Litter size in *G. aurita* in relation to *a)* mean suckling growth rate (data from 11 litters) and *b)* mean age at eye-opening (data from 13 litters). Least squares regression equation in *a)* : mean suckling growth rate ($g.d^{-1}$) = 0.10 - 0.01.litter size (r^2 0.522, p = 0.012).

part of a large litter was simply born prematurely. Therefore, besides *G. aurita*, postpartum oestrus is unknown in any other member of the Tenrecidae, even though it is common in small insectivores of the Soricidae (see Conaway 1958). By suckling the first litter whilst a second litter is developing in the uterus, reproductive output per unit time is increased. Unlike shrew-tenrecs *(Microgale spp)* of comparable body size, which generally come from eastern rain forest habitats (MacPhee 1987), *G. aurita* is found in the arid west and south-west of Madagascar where mean rainfall is low and there is "great irregularity of precipitation from year to year and within individual years" (Donque 1972). Animals in such an unpredictable environment would be expected to reproduce rapidly (see Stearns 1976) during periods of improved food availability asso-

TABLE 3. – Reproductive parameters determined for *G. aurita*. n = number of litters from which reproductive variable was calculated. 'a' = specific fœtal growth rate.

Parameter	n	Range	Mean ± s.e.
Conception date[1]	14	28 Sept.-21 March	30 Nov. ± 14.1 d
Parturition date	13	24 Nov.-29 March	13 Jan. ± 12.0 d
Gestation length (d)	5	54 - ≥69	57[2] ± 1.2
Litter size	13	2 - 5	3.9 ± 0.3
Litter mass (g)	5	1.6 - 3.5	2.7 ± 0.3
Neonate mass (g) at age 1-2 days	5	0.55 - 0.83	0.70 ± 0.05
'a' ($g^{0.33}.d^{-1}$)	5	-	0.02
Suckling growth rate ($g.d^{-1}$)	11	0.021 - 0.090	0.059 ± 0.006
Suckling growth rate ($mm.d^{-1}$)	9	0.55 - 1.01	0.76 ± 0.04
Age at eye-opening (d)	13	21 - 33	24.3 ± 0.9
Age at weaning (d)	7	≥24 ≤51	c. 35
Total number of young per season	7[3]	3 - 10	6.4 ± 1.0

[1] Some dates estimated from mean gestation length. Latest female to conceive (21 March) died in pregnancy.

[2] Mean gestation length calculated from 3 accurate values.

[3] Total number of young per season calculated from 7 females that had the opportunity to breed all summer.

ciated with increased rainfall (Sadlier 1969; Follett 1984). Postpartum oestrus in *G. aurita* may therefore represent an adaptation to an unpredictable environment, optimising reproductive output whilst seasonally favourable conditions prevail. The energetic cost of concurrent pregnancy and lactation in *G. aurita* is not additive (Stephenson and Racey 1993) so there is also an associated energy saving.

Gestation length

Tenrecidae Studies of the usually produce estimates of gestation length within a range of 3-10 days, but between study variation can be large. For example, estimates of gestation length in *Echinops telfairi* range from 50-60 days (Fowler 1986), 61-64 days (Mallinson 1973) and 62-68 days (Eisenberg and Gould 1967). The large variation in

G. aurita gestion length observed in the present study suggests that tenrec gestation is variable. This implies one of the following: 1) a large variation in gestation period between individuals, 2) a longer gestation for first or early litters, 3) a possible delay in fertilisation, implantation or development.

Eisenberg (1975) notes that "tenrecs are capable of showing some true variation in length of gestation" and this may be related to body size or perhaps the "average ambient temperature to which the pregnant female is subjected". He suggests that the shorter gestation length recorded by Mallinson (1973) for *Setifer setosus* bred at Jersey may be accounted for by the higher temperatures at which this zoo maintained its colony. Indeed, Riordan (1972) notes that *S. setosus* gestation "appears to be shorter the higher the ambient temperature". Poppitt (1988) concluded that the variability recorded in *E. telfairi* gestation length "may be explained by the entry into torpor during pregnancy". The occurrence of torpor during gestation probably also extends gestation length in *Tenrec ecaudatus* (Nicoll 1982). Since *G. aurita* is largely heterothermic (Stephenson and Racey 1993), it is possible that torpor was also responsible for arresting the development of some litters in the present study.

Some other mammals have their gestation length affected by external factors (Racey 1981). Racey (1973) showed that pregnant female pipistrelle bats *(Pipistrellus pipistrellus)* deprived of food in cold environments became torpid and their pregnancy was extended by a period similar to that of the induced torpor, indicating that foetal development had been arrested. A variable gestation length was subsequently confirmed in wild pipistrelles (Racey and Swift 1981). In the Norway rat *(Rattus norvegicus)*, females undergoing concurrent pregnancy and lactation on restricted diets often extend the period of the second gestation (Woodside *et al.* 1981). This may be a result of a decrease in *in utero* growth rate.

In some rodents, pregnancies resulting from postpartum matings are prolonged due to delayed implantation (see Amoroso and Perry 1977). In *G. aurita*, pregnancies that occurred concurrently with lactation were shorter so delayed implantation did not occur. The reduced duration of such pregnancies may be a result of the elevated body temperature associated with lactation (Stephenson and Racey 1993).

Gestation length in shrews (Soricidae) of similar size to *G. aurita* is between 20 and 30 days (e.g. Hellwing 1971; Frazer and Hugget 1974; Corbet and Southern 1977; Genoud and Vogel 1990). Although neonate mass in these insectivores is lower than neonate mass in *G. aurita*, the much shorter gestation length in the shrews means their specific foetal growth rate (Frazer and Hugget 1974) is higher at 0.05 - 0.06 $g^{0.33}.d^{-1}$ (Poppitt 1988). Therefore, foetal development in shrews is two to three times faster than in *G. aurita*. The largest tenrec, *Tenrec ecaudatus*, also has a relatively low foetal growth rate when compared with similar-sized insectivores (Frazer and Hugget 1974).

Gestation length in *G. aurita* is within the range found for other tenrec species (Table 4). Therefore, all Tenrecidae have a pregnancy of 50-70 days, irrespective of body mass. This is unusual since gestation length in mammals generally increases with body mass (e.g. Kihlström 1972; Sacher and Staffeldt 1974; Millar 1977; Blueweiss *et al.* 1978; Martin and MacLarnon 1985). The uniformity of Ttenrec gestation length implies that, within the Tenrecidae, this reproductive parameter is influenced by phylogeny.

Litter size

The range of litter size in *G. aurita* (1-5) is the same as in other small Tenrecidae (Table 4) and in tropical shrews (Genoud 1988). Across the Mammalia, larger species

TABLE 4. – Body mass, gestation length and litter size in the Tenrecidae.

Species	Maternal mass (g)	Gestation length (d)	Litter size
Geogale aurita	6.9[1]	54-69[1]	1-5[1,2]
Microgale dobsoni	44.2[3]	58-64[4]	1-5[3]
Microgale talazaci	46.6[3]	58-63[5]	1-3[3,4]
Hemicentetes nigriceps	113.0[3]	55-58[6]	2-4[5]
Hemicentetes semispinosus	133.5[3]	55-63[5]	2-11[5]
Echinops telfairi	175.8[7]	50-68[8,9]	1-10[5]
Setifer setosus	225.0[10]	51-69[11,12]	1-5[5]
Tenrec ecaudatus	900.0[10]	57-64[5]	1-32[5]

Source: [1] This study; [2] Nicoll and Rathbun, 1990; [3] Stephenson, 1991; [4] Eisenberg and Maliniak, 1974; [5] Eisenberg, 1975; [6] Eisenberg and Gould, 1970; [7] Poppitt, 1988; [8] Fowler, 1986; [9] Eisenberg and Gould, 1967; [10] Eisenberg, 1981; [11] Riordan, 1972; [12] Eisenberg and Muckenhirn, 1968.

usually have smaller litters (e.g. Sacher and Staffeldt 1974; French *et al.* 1975; Western 1979; Fleming 1979) though this relationship is far from clear (Millar 1977, 1981) and for species under 1 kg the relationship may be reversed (Tuomi 1980). Within the Tenrecidae, the largest species generally have the highest numbers of neonates per litter (Table 4). Eisenberg (1981) suggests that larger tenrec species may have increased their reproductive rate as a response to predation pressures from carnivores, which replaced them as top predators in Madagascar.

Neonate development

Age at eye-opening in the oryzorictine tenrecs *Microgale talazaci* and *M. dobsoni* is very similar to *G. aurita* (Eisenberg and Gould 1970; Stephenson 1991). However, the *Microgale* species wean on average about one week earlier. Tenrecs in the subfamily Tenrecinae develop more rapidly. Most species reach eye-opening within two weeks of birth and are weaned within three weeks (Eisenberg and Gould 1970). *Hemicentetes* species even reach sexual maturity within 35-40 days of age (Eisenberg 1975). Shrews of similar size to *G. aurita* reach eye-opening between two and three weeks of age and are weaned about a week later (e.g. Hamilton 1944; Crowcroft 1957; Hellwing 1973; Genoud and Vogel 1990). Therefore, postnatal development rate in *G. aurita*, as measured by age at eye-opening and weaning, is similar to that found in other species of its subfamily but slower than in similar-sized shrews.

In *G. aurita*, there was a trend for neonates from smaller litters to be heavier and to grow and develop more rapidly. This conforms with earlier findings (Case 1978) that postnatal growth rate in mammals is dependent on birth weight.

CONCLUSIONS

The present study confirms that gestation length in all Tenrecidae is 50-70 days, irrespective of body mass. Neonate development rates in *G. aurita* are similar to those in other oryzorictine tenrecs but slower than in similar-sized shrews. This suggests that pre and postnatal development rates in the Tenrecidae may be determined by phylogenetic constraints. However, the occurrence of postpartum oestrus in *G. aurita*, a unique phenomenon within the Tenrecidae, may represent an ecological and energetic adaptation to an unpredictable environment.

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