

## **REPRODUCTIVE AND ENERGETIC DIFFERENTIATION OF THE TENRECIDAE OF MADAGASCAR**

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**ABSTRACT.-** The Tenrecidae of Madagascar comprises at least 26 species, all of which are endemic to the island. These species originated from founder stock that colonised from mainland Africa some 60 million years ago and underwent an extensive adaptive radiation to fill a wide range of niches. This paper reviews recent data to determine the energetic and reproductive differentiation that has occurred within this mammalian family and the factors that influenced evolutionary processes. Resting metabolic rate (RMR) is associated with body mass and ecological factors. Small tenrec species that occur in eastern and central forests have RMRs similar to those found in tropical shrews, whereas dry forest and arid zone species have lower than expected RMRs and enter daily or seasonal torpor. The body temperature (T<sub>b</sub>) of non reproductive tenrecs is significantly lower than that of all other insectivores except golden moles. However, RMR and T<sub>b</sub> are elevated in all species of tenrec during pregnancy and lactation, and this may be associated with an improvement in homeothermy. Intraspecific variation in gestation length may be related to the occurrence of daily torpor during pregnancy, a phenomenon previously recorded only in heterothermic microchiropteran bats. Adaptations for increased reproductive output within the constraints of a uniformly long gestation length and low T<sub>b</sub> are discussed. It is concluded that a suite of ecological, climatic and phylogenetic traits are associated with the wide energetic and reproductive differentiation found within the Tenrecidae.

**KEY-WORDS.-** Adaptive radiation, Body temperature, Reproductive energetics, Resting metabolism, Insectivora

**RESUME.-** Les Tenrecidae de Madagascar comprennent au moins 26, espèces toutes endémiques. Ces espèces sont dérivées d'une race colonisatrice, arrivée du continent africain il y a une soixantaine de millions d'années. Aujourd'hui, les descendants de cette race occupent une large gamme de niches écologiques, grâce à une radiation *in-situ* extensive. Cet article rend compte des données récentes acquises sur la différenciation énergétique et reproductive qui s'est produite dans cette famille de mammifères, et des facteurs impliqués dans ces processus évolutifs. Le taux métabolique en repos (TMR) est corrélé au poids corporel et aux facteurs écologiques. Les espèces de petits tenrecs qui vivent dans les forêts centrales et orientales montrent des valeurs de TMR similaires à ceux des musaraignes tropicales. Au contraire, les espèces vivant dans les forêts sèches et dans les zones arides montrent des valeurs de TMR plus faibles que celles attendues; ces espèces montrent une torpeur quotidienne ou saisonnière. Les valeurs de température du corps (TC) des tenrecs dans la phase non-reproductive sont significativement inférieures à celles de toutes les autres espèces d'insectivores, à part la taupe dorée. Néanmoins, chez toutes les espèces de tenrecs, les valeurs de TMR et TC sont plus élevées pendant les phases de grossesse et de lactation; ceci est peut-être lié à une amélioration d'homothermie. La variation intraspécifique de la durée de gestation est peut-être liée à la torpeur quotidienne de la grossesse, phénomène considéré jusqu'à maintenant comme spécifiquement limité aux microchiroptères hétérothermiques. Les adaptations qui augmentent la production reproductive sous les contraintes d'une

faible TC et d'une durée de gestation uniforme et longue, sont discutées. En conclusion, il semble que des caractères écologiques, climatiques, et phylogénétiques sont liés à la différenciation extensive énergétique et reproductive qui se existe dans la famille Tenrecidae.

**MOTS-CLES.-** Radiation adaptative, Temperature corporelle, Energie reproductrice, Metabolisme du repos, Insectivora

## INTRODUCTION

### THE TENRECIDAE

The Tenrecidae (Mammalia: Insectivora) is an ancient lineage of eutherian mammals. The family is comprised of three subfamilies, the Tenrecinae and Oryzorictinae of Madagascar, with eight genera and 26 species, and the Potamogalinae (otter-shrews) of west and central Africa, with two genera and three species (GENEST & PETTER, 1974; CORBET & HILL, 1991; STEPHENSON, 1995). Some authorities classify otter-shrews as a separate family (e.g. EISENBERG, 1981). The Tenrecidae shows close affinities with the Chrysochloridae, the African golden moles (VAN VALEN, 1967), and it has been suggested that the Chrysochloridae and Tenrecidae were early offshoots from the lineage that gave rise to the Insectivora (EISENBERG, 1981).

Malagasy tenrecs originated on mainland Africa where fossil tenrecids have been found in the Miocene deposits of Kenya (BUTLER & HOPWOOD, 1957; BUTLER, 1969). Madagascar probably split from mainland Africa about 165 million years ago, and reached its present position around 121 million years ago during the Cretaceous (RABINOWITZ *et al.*, 1983). Since this separation predates the modern mammal fauna, all mammalian taxa must have colonized the island by crossing the Mozambique Channel. Although the earliest insectivores probably reached the island by rafting in the Palaeocene around 60 million years ago (SIMPSON, 1940), it is unclear which form or forms of tenrec first invaded Madagascar. The genus *Geogale* is represented in the fossil record on Africa (BUTLER & HOPWOOD, 1957) but it is too specialised to have given rise to the family and it is likely that there was more than one founding stock. The original tenrec colonists would have probably included unspecialised animals with a conservative body plan but, in isolation on Madagascar, they underwent an extensive adaptive radiation (EISENBERG & GOULD, 1970). Consequently, Malagasy representatives of the family are morphologically and ecologically diverse. They range in body mass from 4 g (*Microgale pulla*) to over 2 kg (*Tenrec ecaudatus*), and have evolved to inhabit niches in eastern rainforest (e.g. *Microgale talazaci*, *Hemicentetes semispinosus*), central plateau forest (e.g. *M. dobsoni*, *H. nigriceps*), and south-western dry forests (e.g. *Echinops telfairi*, *Geogale aurita*). Most species are terrestrial though species in the genus *Oryzorictes* are adapted for a semi-fossorial life style and *Limnogale mergulus* is aquatic.

The extensive adaptive radiation of the Tenrecidae led to the evolution of a variety of reproductive and energetic strategies within the family. For example, some species (e.g. *T. ecaudatus*, *H. semispinosus*) breed at an early age and produce large litters, whereas other species (e.g. *M. talazaci*, *G. aurita*) have smaller litters that exhibit relatively slow development rates (EISENBERG & GOULD, 1970; STEPHENSON, 1991,

1993; STEPHENSON *et al.*, 1994). Many species of tenrec are heterothermic so metabolic rate measured under standard conditions is referred to as resting metabolic rate (RMR) instead of basal metabolic rate (BMR) (STEPHENSON, 1991; STEPHENSON & RACEY, 1993a). Recent studies have shown that, although some species maintain RMR at a level below that expected from body mass (NICOLL & THOMPSON, 1987; STEPHENSON & RACEY, 1993a,b, 1994), other species maintain RMR at levels expected from body mass or even higher (STEPHENSON & RACEY, 1993b; STEPHENSON, 1994a,b). The diversity of reproductive strategies and variability in RMR within the Tenrecidae make this family an ideal model on which to investigate the influence of metabolic rate on life history strategy.

### REPRODUCTIVE ENERGETICS OF EUTHERIAN MAMMALS

RMR (or BMR in homeothermic species) is a frequently used physiological variable because it is easily measurable under laboratory conditions and comparable between taxa. RMR is strongly correlated with body mass across the Mammalia (*e.g.* KLEIBER, 1961; MCNAB, 1988). Interspecific variations in RMR not accounted for by body mass have been attributed to differences in food habits, activity levels and climate (*e.g.* MCNAB, 1978, 1980, 1983, 1986, 1992; HENNEMANN *et al.*, 1983; DANIELS, 1984; MULLER, 1985). For example, large eutherians that feed on vertebrates, nuts or grass and forbs generally have high RMR relative to their body mass, whilst species that feed on invertebrates, fruits, seeds and leaves of woody plants generally have lower rates (MCNAB, 1986). In addition, it has been suggested that many of the ecological correlates of RMR may also be taxonomic associations (ELGAR & HARVEY, 1987).

Many investigators have observed that eutherian mammals with higher RMR produce more offspring which have faster prenatal and postnatal development rates (*e.g.* MCNAB, 1980, 1986; OFTEDAL, 1984; GLAZIER, 1985). Recent studies that have removed the effects of body mass suggest that the relationship between metabolism and life histories may vary between taxa (STEPHENSON & RACEY, 1995) or may not be apparent at all (READ & HARVEY, 1989).

Ambient temperature ( $T_a$ ) can influence body temperature ( $T_b$ ) in heterothermic mammals, and in turn can influence RMR (*e.g.* STEPHENSON & RACEY, 1993b), although the direct relationship between  $T_b$  and RMR is difficult to distinguish. In a few heterothermic species, fluctuating  $T_b$  associated with entry into torpor can sometimes affect gestation length (*e.g.*, RACEY, 1973; RACEY & SWIFT, 1981; STEPHENSON & RACEY, 1993a). However, to date there has been no analysis of the potential influence of  $T_b$  on reproductive or energetic strategies in tenrecs.

This paper reviews recent data on the Tenrecidae to provide an overview of reproductive energetics within the Insectivora and factors that influence metabolism and reproduction. It also examines the influence of body temperature on energetic and life history strategies.

## REPRODUCTIVE ENERGETICS OF THE TENRECIDAE

### Resting metabolic rate

Resting metabolic rate in the Tenrecidae scales to body mass (Fig. 1). Residual variation in the RMR-mass curve cannot be explained with certainty given the difficulty in determining cause and effect. However, it may have ecological significance. For example, reduced levels of RMR have been well documented in desert-dwelling rodents (see *e.g.* HULBERT *et al.*, 1985; HAIM & BORUT, 1986) and shrews (LINDSTEDT, 1980). It is therefore notable that the two species of tenrec from the hot, arid south-west of Madagascar (*G. aurita* and *E. telfairi*) have substantially lower levels of mean RMR than other tenrecs relative to their body size (Fig. 1). The incorporation of termites in the diet of *G. aurita* may also affect RMR (MCNAB, 1984). The aquatic tenrec, *Limnogale mergulus*, does not appear to maintain RMR at a significantly higher level than other tenrec species (STEPHENSON, 1994a). This contrasts with the trend identified in other aquatic vertebrates which normally maintain RMR at levels higher than expected from body mass (*e.g.* MCNAB 1978, 1986; BENNETT & HARVEY, 1987). However, when compared with other marsupials, the water opossum, *Chironectes minimus*, also shows no elevated level of metabolic rate (THOMPSON, 1988). Therefore, the association between elevated RMR and aquatic habits may not be uniform throughout the Mammalia. Water shrews are amongst the largest species of temperate zone soricids (GENOUD, 1988). This may provide them with a greater thermal inertia to reduce the loss of body heat when in water. *L. mergulus* is the largest of the oryzorictine tenrecs so a reduction in thermal inertia through increased body size, rather than elevated metabolic rate, may be the main adaptation of the species to an aquatic mode of life. The fossorial *O. hova* also has a relatively high RMR (Fig. 1). An elevated RMR is found in other small fossorial insectivores (MCNAB, 1979; CONTRERAS & MCNAB, 1990) and is probably associated with the maintenance of homeothermy (MCNAB, 1983) rather than the niche these species inhabit.

Further evidence for the potential effects of climate on metabolism can be found in the Insectivora. Shrews of the subfamily Soricinae have higher RMR than species of the Crocidurinae. The main difference between the two sub-families can most likely be explained by evolution in geographical isolation under differential climatic conditions: the Crocidurinae having evolved in tropical Africa and the Soricinae in temperate Eurasia (VOGEL, 1976).

Those tenrec species which enter seasonal torpor, in general have lower RMRs. Seasonal hypothermia is unusual in the tropics but has been recorded in six tenrec species: *G. aurita*, *H. semispinosus*, *H. nigriceps*, *S. setosus*, *E. telfairi* and *T. ecaudatus* (GOULD & EISENBERG, 1966; EISENBERG & GOULD, 1970; STEPHENSON & RACEY, 1994). Further research is required to determine the influence of endogenous and exogenous rhythms on the occurrence of torpor within the Tenrecidae but in some species it is likely that any endogenous rhythm that exists is entrained by ambient temperature or photoperiod (STEPHENSON & RACEY, 1994).

When compared with insectivores of similar body mass, RMR in tenrecs is generally lower, though there are exceptions to the rule. For example, shrew-tenrecs of the genus *Microgale* have RMRs lower than shrews of the Soricinae, but a similar level

to tropical shrews of the Crocidurinae (see STEPHENSON & RACEY, 1995). Reliable data on RMR are only available for five species of Erinaceidae which range in body mass from 400 to 750g (see STEPHENSON, 1991). *T. ecaudatus* is the only tenrec within this mass range but even though the largest erinaceids are smaller than *T. ecaudatus*, they have higher RMR (STEPHENSON, 1991). Further data are required on the more closely related Chrysochloridae to establish how their level of RMR compares with tenrecines.

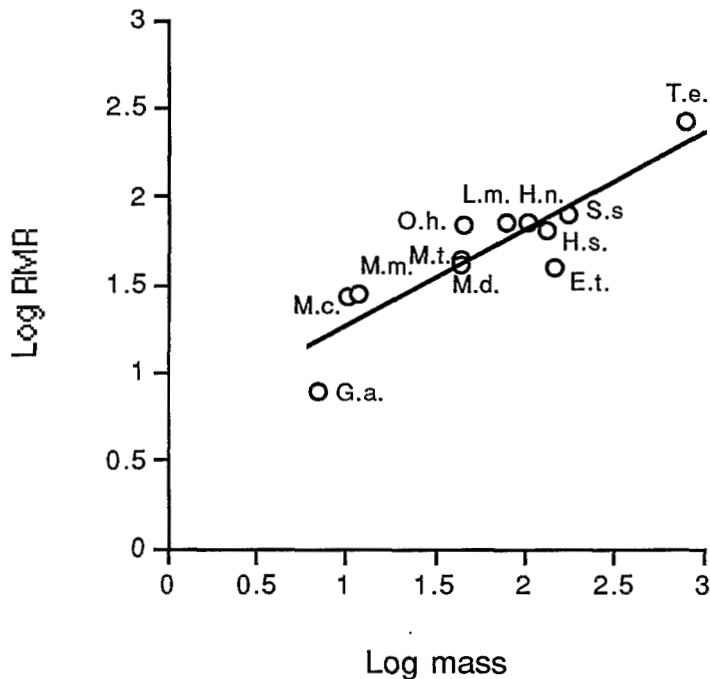


Figure 1. Log-log plot of resting metabolic rate against body mass in the Tenrecidae. Least squares regression equation:  $y = 0.548x + 0.724$  ( $r^2 = 0.77$ ). Tenrec species: *G.a.* = *Geogale aurita*; *M.c.* = *Microgale cowani*; *M.m.* = *M. melanorrhachis*; *M.t.* = *M. talazaci*; *M.d.* = *M. dobsoni*; *O.h.* = *Oryzorictes hova*; *L.m.* = *Limnogale mergulus*; *H.n.* = *Hemicentetes nigriceps*; *H.s.* = *H. semispinosus*; *E.t.* = *Echinops telfairi*; *T.e.* = *Tenrec ecaudatus*. Data from Stephenson (1994a,b), and Stephenson & Racey (1993a,b, 1994).

### Body temperature and homeothermy

Body temperature in most species of tenrec is affected by  $T_a$  (EISENBERG & GOULD, 1970; STEPHENSON & RACEY, 1993b). In some species there is no readily defined point at which there is a shift from homeothermy to heterothermy since there is no obvious  $T_b$  at which the animals enter torpor (POPPITT *et al.*, 1994). On the basis of data collected to date, it is possible to identify a continuum of homeothermic capacities and energetic strategies across the family. This ranges from species such as *G. aurita* and *E. telfairi* that are not continuously homeothermic at any  $T_a$  and enter daily and seasonal torpor, to species such as *M. cowani*

and *M. melanorrhachis* that maintain relatively constant Tb and RMR (STEPHENSON & RACEY, 1993b).

If Tb in tenrecs maintained at Ta 25-30°C (the nearest approximation to a thermoneutral zone in species that maintain homeothermy) is compared with other insectivores maintained in thermoneutral conditions, tenrecs have a significantly lower mean Tb than all other taxa (T-test,  $p < 0.05$ ), with the exception of the closely related Chrysochloridae (Figure 2). Even those tenrec species, such as *M. cowani* and *O. hova*, that maintain RMR at a level close to that expected from body mass, have low Tb. This implies that, even when RMR is relatively high, tenrecs cannot maintain Tb at levels found in other Insectivora.

## Reproduction

Within the Tenrecidae, there is a wide range of reproductive strategies (see EISENBERG & GOULD, 1970; STEPHENSON, 1991, 1993; STEPHENSON *et al.*, 1994). Interspecific variation is evident in most traits (see STEPHENSON & RACEY, 1995, for data summary). For example, mean litter size ranges from 2.8 in *H. nigriceps* to 16.6 in *T. ecaudatus*. In *H. semispinosus*, the mean age of eye-opening is 8.5 days and individuals wean within three weeks, attaining reproductive maturity within 35-40 days of birth (EISENBERG, 1975). In contrast, *G. aurita* neonates have a mean age at eye-opening of 24 days and wean after five weeks (STEPHENSON, 1993). Some of the variability in life histories can be accounted for by body mass which is correlated with variables such as neonate mass and maximum litter size (STEPHENSON & RACEY, 1995). However, most life history variables in the Tenrecidae are not significantly related to body mass.

Across the Mammalia, gestation length is closely correlated with maternal body mass (READ & HARVEY, 1989) but no such correlation is evident in the Tenrecidae. Across the body mass range, gestation length is between 50 and 70 days (see STEPHENSON, 1993) and considerable intraspecific variation is apparent, as exemplified by *G. aurita* which had one confirmed gestation period of 54 days, and another of more than 69 days (STEPHENSON, 1993). When compared with other Insectivora of similar body size, tenrec gestation length is much longer than expected. For example, *G. aurita* (mean body mass 6.9g) has a mean gestation length of 61.5 days, whereas a similar-sized shrew, *Cryptotis parva* (6.4g) has a gestation length of 22 days (see STEPHENSON & RACEY, 1995). In general, shrews have gestation lengths between 3 and 4 weeks, and larger insectivores such as hedgehogs and moles have gestation lengths of about 5 weeks (STEPHENSON, 1991). In contrast, all tenrecs have gestation lengths of around 8 weeks. The uniformly long gestation length in tenrecs does not produce more precocial young since neonates of all species are born blind and with a closed auditory meatus. The specific foetal growth velocity (a measure of prenatal development rate, HUGGETT & WIDDAS, 1951) is also lower than expected (STEPHENSON, 1991). Postnatal development rates differ between subfamilies. Oryzoricines have postnatal development rates lower than shrews of similar size (see STEPHENSON, 1993). However, the Tenrecinae often have more rapid postnatal development rates than other Insectivora. For example, the eyes of neonatal tenrecs generally open within 2 weeks of parturition, more rapidly than any other large insectivores and even more rapidly than many shrew species (STEPHENSON, 1991).

*G. aurita* is the only species in the Tenrecidae known to experience post-partum oestrus, a consequence of which is that a female is able to suckle one litter while a second develops in the uterus. This phenomenon may represent an adaptation to an unpredictable environment, optimising reproductive output whilst seasonally favourable conditions prevail (STEPHENSON, 1993). Since the energetic costs of concurrent pregnancy and lactation are not additive (STEPHENSON & RACEY, 1993a), it is also associated with an energy saving.

### Reproduction, RMR and Tb

All species of tenrec studied to date have shown a mass-independent increase in RMR during reproduction (NICOLL & THOMPSON, 1987; STEPHENSON & RACEY, 1993a,b, 1994; THOMPSON & NICOLL, 1986). This increase is associated with the maintenance of homeothermy (STEPHENSON & RACEY, 1993a,b, 1994; POPPITT *et al.*, 1994) and higher or more constant body temperatures have been recorded in a number of tenrec species during reproduction (EISENBERG & GOULD, 1967; NICOLL, 1982; POPPITT, 1988; STEPHENSON & RACEY, 1993a,b). Increased and less variable body temperatures have also been recorded during reproduction in other heterothermic eutherians such as hedgehogs (FOWLER, 1988) and bats (*e.g.* AUDET & FENTON, 1988; STUDIER & O'FARRELL, 1972). Therefore, maintenance of homeothermy or elevation of body temperature may be essential for reproduction in heterothermic eutherians. The advantages of higher and more constant Tb are unclear but may be associated with a faster rate of foetal development (RACEY, 1973; STEPHENSON & RACEY, 1993a) and a subsequent increase in reproductive potential. However, the maintenance of homeothermy is energetically expensive (MCNAB, 1983) and will add to the cost of reproduction. The increase in RMR during pregnancy and lactation may therefore reflect the energy expenditure necessary to improve thermoregulation. Conversely, an elevated Tb may simply be a corollary of an increased metabolic rate inherently associated with reproduction. A full understanding of reproductive energetics in heterothermic eutherians will arise only after the inter-relationship between metabolic rate and Tb has been established.

There is evidence that some tenrec species such as *G. aurita* and *E. telfairi* sometimes enter torpor during pregnancy (NICOLL & THOMPSON, 1987; STEPHENSON & RACEY, 1993a). 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 experiencing different climatic conditions from year to year (RACEY & SWIFT, 1981). It is relevant in this respect that *G. aurita* also has variable gestation length and since it is largely heterothermic (STEPHENSON & RACEY, 1993a), it is possible that torpor is also responsible for arresting the development of some litters.

When reproductive variables for the Tenrecidae are compared with RMR, and the effects of body mass are removed, there is no significant relationship between energy expenditure and reproductive output either within or between species (STEPHENSON & RACEY, 1993b, 1995). However, when a similar analysis is conducted on shrews, an interspecific difference is revealed, with those species with higher metabolic rates producing more young at a faster rate. So why can shrews with relatively high RMR

have a relatively greater reproductive output, yet no such advantage occur in tenrecs? Four reasons have been suggested (STEPHENSON & RACEY, 1995):

**1) Phylogeny.** Gestation length is uniformly long across the family. Many species also have similar postnatal development rates with the result that age at eye-opening and age at weaning are not dependent on body mass. This implies that some elements of tenrec life histories may be constrained by phylogeny rather than body size or energy metabolism (STEPHENSON, 1993).

**2) Maternal metabolism.** All tenrec species increase RMR during reproduction. Therefore, perhaps maternal RMR during pregnancy and lactation, and its relative increase above non-breeding levels, is a better indication of energy allocated to reproduction. However, to date, RMR in gestation and lactation has been determined in too few species, to permit interspecific analysis.

**3) Limited residual variation in RMR.** RMR is more closely related to body mass in the Tenrecidae than in the Soricidae. The more limited residual variation in RMR among tenrecs may have reduced the probability of a discernible relationship between RMR and reproductive variables.

**4) Body temperature.** Increased RMR in tenrec species during reproduction may be associated more with an improvement in homeothermy than with any increase in reproductive rate (STEPHENSON & RACEY, 1993a,b). Body temperature may be a simple corollary of RMR but it may also influence mammalian reproduction independently. In pregnant heterothermic bats, reduction of body temperature during torpor extends gestation length (RACEY, 1973; RACEY & SWIFT, 1981), and a similar phenomenon may occur in at least one tenrec species (STEPHENSON & RACEY, 1993a). The uniformly low  $T_b$  in tenrecs (as demonstrated in Fig. 2) also implies some phylogenetic constraint, and the inability of species to raise  $T_b$  to levels found in other Insectivora may be one factor preventing increased reproductive output with increased RMR. Further investigation of the relationship between thermoregulatory capacity and life history parameters in the Tenrecidae may determine the relative importance of body temperature to mammalian reproduction.

In shrews, the relationship between RMR and reproduction may not be causal. Tropical species have lower RMR and lower reproductive output, and this is thought to be due to their evolution in different climates. However, reproductive and energetic strategies in shrew subfamilies may have evolved independently under different and unrelated selection pressures. For example, temperate zone shrews (Soricinae) may have evolved an elevated RMR as a result of selection pressure to maintain homeothermy in environments with low ambient temperatures. In contrast, faster reproductive rates in these species may have evolved in response to the restricted breeding seasons at temperate latitudes.

THOMPSON (1992) suggests that, if species with a relatively high metabolic rate allocate more energy to reproduction, there are two alternative strategies. Some species with high RMR « will have opted for greater speed, others will have opted for greater effort, and some may have opted for moderate increases in both speed and effort ». Results from the Tenrecidae (STEPHENSON & RACEY, 1995) suggest that some species with high RMR are incapable of increasing speed or effort. However, those species that avoid torpor may reduce gestation length. In some tenrec species, avoidance of seasonal torpor when suitable conditions prevail can lead to winter breeding (STEPHENSON & RACEY, 1994). Although daily torpor does occur during reproduction in some species



(NICOLL & THOMPSON, 1987; STEPHENSON & RACEY, 1993a), probably as an adaptation to adverse conditions of food availability or climate, avoidance or reduction of torpor in pregnant tenrecs may maintain rates of foetal development (STEPHENSON & RACEY, 1993a).

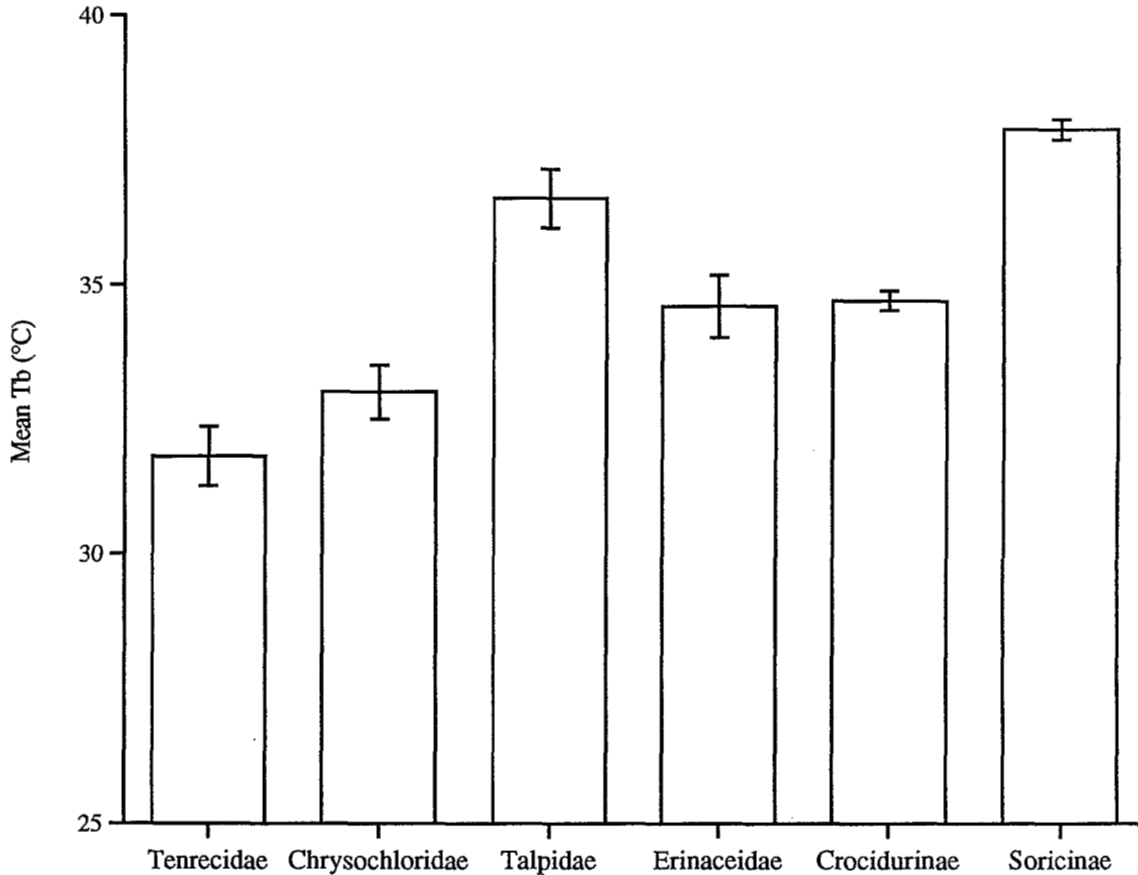


Figure 2. Body temperature in the Insectivora. Data sources listed in Stephenson (1991) and Stephenson and Racey (1993a, b; 1994).

Overall, therefore, the selective advantage in high RMR may be the maintenance of daily or year-round activity, increasing opportunities to reproduce and reducing inter-birth intervals, rather than more directly increasing reproductive output through, for example, faster development rates or higher fecundity.

There is much evidence to suggest that mortality patterns, measured by variables such as probability of survival at birth and life expectancy, are the strongest predictors of life history besides body mass (*e.g.* HARVEY & ZAMMUTO, 1985; HARVEY *et al.*, 1989, 1991; CHARNOV, 1991). Therefore, if RMR does have any influence on reproduction, it might be expected to be associated with these life history variables. More data are required on the lifespans of free-living insectivores to facilitate such analysis.

## CONCLUSIONS

Mammalian reproduction is energetically expensive (LOUDON & RACEY, 1987; GITTLEMAN & THOMPSON, 1988; THOMPSON, 1992) but the relationship between metabolism and reproduction is complex and difficult to discern and may have taxonomic differences. Cause and effect are unclear and life histories may have evolved under different constraints to RMR. Maternal RMR may have a greater influence on life histories than RMR of non-breeding individuals. Future studies need to measure RMR for more species during pregnancy and lactation and to record life history variables concurrently. Detailed information on thermoregulation within the Insectivora may also help to distinguish between the potentially different effects of body temperature and RMR on reproduction.

It can be concluded that a suite of ecological, climatic and phylogenetic traits are associated with the wide energetic and reproductive differentiation found within the Tenrecidae, one of the broadest adaptive radiations to have occurred in any mammalian family. Continued study of this ancient eutherian lineage may therefore improve our understanding of the evolution of reproductive and energetic strategies within the Mammalia.

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## REFERENCES

- AUDET, D. & M.B. FENTON, 1988. Heterothermy and use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): a field study. *Physiol. Zool.*, 61: 197-204.
- BENNETT, P.M. & P.H. HARVEY, 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool. Lond.*, 213: 327-363.
- BUTLER, P.M., 1969. Insectivores and bats from the Miocene of East Africa: new material. *In*: L.S.B. Leakey (ed.), *Fossil vertebrates of Africa, Volume 1*. pp. 1-38. Academic Press, New York.
- BUTLER, P.M. & A.T. HOPWOOD, 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. *Fossil mammals of Africa 13*. British Museum (Natural History), London.
- CHARNOV, E.L., 1991. Evolution of life history variation among female mammals. *Proc. Nat. Acad. Sc., USA*, 88: 1134-1137.
- CONTRERAS, L.C. & B.K. MCNAB, 1990. Thermoregulation and energetics in subterranean mammals. *In*: E. Nevo & O.A. Reig (eds.), *Evolution of subterranean mammals at the organismal and molecular levels*. pp. 231-250. Alan Liss Inc, New York.

- CORBET, G.B. & J.E. HILL, 1991. A World List of Mammalian Species. Third Edition. British Museum (Natural History), London and Oxford University Press, Oxford.
- DANIELS, H.L., 1984. Oxygen consumption in *Lemur fulvus*: deviations from the ideal model. *J. Mammal.*, 65: 584-592.
- EISENBERG, J.F., 1975. Tenrecs and solenodons in captivity. *Int. Zoo Yearbook*, 15: 6-12.
- EISENBERG, J.F., 1981. The Mammalian Radiations. Athlone Press, London.
- EISENBERG, J.F. & E. GOULD, 1967. The maintenance of tenrecoid insectivores in captivity. *Int. Zoo Yearbook*, 7: 194-196.
- EISENBERG, J.F. & E. GOULD, 1970. The tenrecs: a study in mammalian behavior and evolution. *Smithson. Contribs. Zool.*, 27: 1-127.
- ELGAR, M.A. & P.H. HARVEY, 1987. Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Funct. Ecol.*, 1: 22-36.
- FOWLER, P.A. 1988. Thermoregulation in the female hedgehog, *Erinaceus europaeus*, during the breeding season. *J. Reprod. Fert.*, 82: 285-292.
- GENEST, H. & F. PETTER, 1974. Part 1.1: Family Tenrecidae. *In*: J. Meester & H.W. Setzer (eds.), *The mammals of Africa: an identification manual*. pp. 1-7. Smithsonian Institution Press, Washington DC.
- GENOUD, M., 1988. Energetic strategies of shrews: ecological constraints and evolutionary implications. *Mammal Rev.*, 18: 173-193.
- GITTLEMAN, J.L., & S.D. THOMPSON, 1988. Energy allocation in mammalian reproduction. *Am. Zool.*, 28: 863-875.
- GLAZIER, D.S., 1985. Energetics of litter size in five species of *Peromyscus* with generalizations for other mammals. *J. Mammal.*, 66: 629-642.
- GOULD, E. & J.F. EISENBERG, 1966. Notes on the biology of the Tenrecidae. *J. Mammal.*, 47: 660-686.
- HAIM, A. & A. BORUT, 1986. Reduced heat production in the bushy-tailed gerbil *Sekeetamys calurus* (Rodentia) as an adaptation to arid environments. *Mammalia*, 50: 27-33.
- HARVEY, P.H., PAGEL M.D. & J.A. REES, 1991. Mammalian metabolism and life histories. *Am. Nat.*, 137: 556-566.
- HARVEY P.H., READ A.F. & E.L. PROMISLOW, 1989. Life history variation in placental mammals: unifying the data with the theory. *In*: P.H. Harvey & L. Partridge (eds.), *Oxford Surveys in Evolutionary Biology*, Volume 6. pp. 13-31. Oxford University Press, Oxford.
- HARVEY, P.H. & R.M. ZAMMUTO, 1985. Patterns of mortality and age at first reproduction in natural populations of mammals. *Nature, Lond.*, 15: 319-320.
- HEIM DE BALSAC, H., 1972. Insectivores. *In*: R. Battistini & G. Richard-Vindard (eds.), *Biogeography and ecology in Madagascar*. pp. 629-660. W. Junk, The Hague.
- HENNEMANN, W.W., III, THOMPSON, S.D. & M.J. KOENECNY, 1983. Metabolism of crab-eating foxes *Cerdocyon thous*: ecological influences on the energetics of canids. *Physiol. Ecol.*, 56: 319-324.
- HUGGETT, A. St.G & WIDDAS, W.F., 1951. The relationship between mammalian foetal weight and conception age. *J. Physiol.*, 114: 306-317.

- HULBERT, A.J., D.S. HINDS & R.E. MacMILLEN, R.E., 1985. Minimal metabolism, summit metabolism and plasma thyroxine in rodents from different environments. *Comp. Biochem. Physiol.*, 81: 687-693.
- KLEIBER, M., 1961. *The fire of life: an introduction to animal energetics*. John Wiley, New York.
- LINDSTEDT, S.L., 1980. Energetics and water economy of the smallest desert mammal. *Physiol. Zool.*, 53: 82-97.
- LOUDON, A.S.I. & P.A. RACEY (eds.), 1987. *Reproductive energetics in mammals*. Symp. zool. Soc., Lond., No.57. Oxford University Press, Oxford.
- McNAB, B.K., 1978. The comparative energetics of neotropical marsupials. *J. Comp. Physiol.*, 125: 115-128.
- McNAB, B.K., 1979. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. *Ecology*, 60: 1010-1021.
- McNAB, B.K., 1980. Food habits, energetics and the population biology of mammals. *Am. Nat.*, 116: 106-124.
- McNAB, B.K., 1983. Energetics, body size, and the limits to endothermy, *J. Zool., Lond.*, 199: 1-29.
- McNAB, B.K., 1984. Physiological convergence amongst ant-eating and termite-eating mammals. *J. Zool., Lond.*, 203: 485-510.
- McNAB, B.K., 1986. The influence of food habits in the energetics of eutherian mammals. *Ecol. Monographs*, 56: 1-9.
- McNAB, B.K., 1988. Complications inherent in scaling the basal rate of metabolism in mammals. *Quart. Rev. Biol.*, 63: 25-54.
- McNAB, B.K., 1992. A statistical analysis of mammalian rates of metabolism. *Funct. Ecol.*, 6: 672-279.
- MULLER, E.F., 1985. Basal metabolic rates in primates - the possible role of phylogenetic and ecological factors. *Comp. Biochem. Physiol.*, 81A: 707-711.
- NICOLL, M.E., 1982. *Reproductive Ecology of Tenrec ecaudatus (Insectivora: Tenrecidae) in the Seychelles*. Unpublished Ph.D. thesis, University of Aberdeen, Aberdeen, U.K..
- NICOLL, M.E. & S.D. THOMPSON, 1987. Basal metabolic rates and energetics of reproduction in therian mammals: marsupials and placentals compared. *Symp. zool. Soc. Lond.*, No. 57: 7-27.
- OFTEDAL, O.T., 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symp. zool. Soc., Lond.*, No. 51: 33-85.
- POPPITT, S.D., 1988. *Energetics of Reproduction and Overwintering in some Insectivorous Mammals (Mammalia: Insectivora)*. Unpublished Ph.D. thesis, University of Aberdeen, U.K..
- POPPITT, S.D., SPEAKMAN, J.R. & P.A. RACEY, 1994. Energetics of reproduction in the lesser hedgehog tenrec, *Echinops telfairi* (Martin). *Physiol. Zool.*, 67: 976-994.
- RABINOWITZ, P.D., COFFIN, M.F. & D. FALVEY, 1983. The separation of Madagascar and Africa. *Science*, 220: 67-69.
- RACEY, P.A., 1973. Environmental factors affecting the length of gestation in heterothermic bats. *J. Reprod. Fert., Suppl.*, 19: 175-189.
- RACEY, P.A. & S.M. SWIFT, 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. *J. Reprod. Fert.*, 61: 123-129.

- READ, A.F. & P.H. HARVEY, 1989. Life history differences among the eutherian radiations. *J. Zool., Lond.*, 219: 329-353.
- SIMPSON, G.G. 1940. Mammals and land bridges. *J. Washington Acad. Sci.*, 30: 137-163.
- STEPHENSON, P.J. 1991. Reproductive energetics of the Tenrecidae (Mammalia: Insectivora). Unpublished PhD thesis, University of Aberdeen, Aberdeen, U.K.
- STEPHENSON, P.J., 1993. Reproductive biology of the large-eared tenrec, *Geogale aurita* (Insectivora: Tenrecidae). *Mammalia*, 57: 553-563.
- STEPHENSON, P.J., 1994a. Resting metabolic rate and body temperature in the aquatic tenrec, *Limnogale mergulus* (Insectivora: Tenrecidae). *Acta Theriol.*, 39: 89-92.
- STEPHENSON, P.J., 1994b. Notes on the biology of the fossorial tenrec, *Oryzorictes hova* (Insectivora: Tenrecidae). *Mammalia*, 58(2): 312-315.
- STEPHENSON, P.J. 1995. Taxonomy of shrew-tenrecs (*Microgale* spp.) from eastern and central Madagascar. *J. Zool., Lond.*, 235: 339-350.
- STEPHENSON, P.J. & P.A. RACEY, 1993a. Reproductive energetics of the Tenrecidae (Mammalia: Insectivora). I. The large-eared tenrec, *Geogale aurita*. *Physiol. Zool.*, 66: 643-663.
- STEPHENSON, P.J. & P.A. RACEY, 1993b. Reproductive energetics of the Tenrecidae (Mammalia: Insectivora). II. The shrew-tenrecs, *Microgale* spp. *Physiol. Zool.*, 66: 664-685.
- STEPHENSON, P.J. & P.A. RACEY, 1994. Seasonal variation in resting metabolic rate and body temperature of streaked tenrecs, *Hemicentetes nigriceps* and *H. semispinosus* (Insectivora: Tenrecidae). *J. Zool., Lond.*, 232: 285-294.
- STEPHENSON, P.J. & P.A. RACEY, 1995. Resting metabolic rate and reproduction in the Insectivora. *Comp. Biochem. Physiol.*, 112A: 215-223.
- STEPHENSON, P.J., RACEY, P.A. & F. RAKOTONDRAPARANY, 1994. Maintenance and reproduction of tenrecs (Tenrecidae) in captivity at Parc Tsimbazaza, Madagascar. *Int. Zoo Yearbook*, 33: 194-201.
- STUDIER, E.M. & M.J. O'FARRELL, 1972. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) I. Thermoregulation. *Comp. Biochem. Physiol.*, 41A: 567-595.
- THOMPSON, S.D., 1988. Thermoregulation in the water opossum (*Chironectes minimus*): an exception that 'proves' a rule. *Physiol. Zool.*, 61: 450-460.
- THOMPSON, S.D., 1992. Energetics of gestation and lactation in small mammals: basal metabolic rate and the limits of energy use. *In*: T.E. Tomasi & T.H. Horton (eds). *Mammalian Energetics: Interdisciplinary Views of Metabolism and Reproduction*. pp. 213-259. Cornell Univ. Press, Ithaca, New York.
- THOMPSON, S.D. & M.E. NICOLL, 1986. Basal metabolic rate and energetics of reproduction in therian mammals. *Nature, Lond.* 321: 690-693.
- VAN VALEN, L., 1967. New Paleocene insectivores and insectivore classification. *Bull. Am. Mus. Nat. Hist.*, 135: 219-284.
- VOGEL, P., 1976. Energy consumption of European and African shrews. *Acta Theriol.*, 13: 195-206.