



Tall Tales of a Tropical Squirrel

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Emily Mae Meijaard¹, Rona Anne Dennis² and Erik Meijaard^{3,4}

¹ British International School-Jakarta, Jakarta, Indonesia; Email: emily.meijaard@gmail.com

² Country Woods 306, Jakarta, Indonesia

³ People and Nature Consulting International, Jakarta, Indonesia

⁴ School for Archaeology and Anthropology, Australian National University, Canberra, Australia

The Tufted Ground Squirrel, *Rheithrosciurus macrotis* is an endemic of the South East Asian island of Borneo. This species is remarkable in several aspects. Phylogenetic research indicates that its nearest living relatives are a group of South American squirrel species (Mercer & Roth, 2003). It is unclear how the evolutionary lineage leading to *Rheithrosciurus* ended up on Borneo without leaving behind any known relatives on either the Asian or North American land masses. The lineage of ancestors of *Rheithrosciurus* occupying Eurasia is either extinct without known fossil remains or the genus supposedly colonized Borneo in an independent long-distance colonization event (Mercer & Roth, 2003). More recent studies indicate that the *Rheithrosciurus* lineage diverged from a group of Palaearctic species of the genus *Sciurus* as early as 36 million years ago, and colonized Borneo overland from South East Asia (Pečnerová & Martínková 2012).

Morphologically, *Rheithrosciurus* is also unusual. Its baculum is similar to that in the genus *Sciurus*, the squirrels of Eurasia, North and South America, but unlike those found in other South East Asian squirrels (Thomas, 1915; Zahn, 1941), while its longitudinally grooved incisors also remind one of *Sciurus* (Gray, 1867). Then, there is its club-shaped tail (Gray, 1867). Several early naturalists commented on the spectacularly large tail of *Rheithrosciurus* (Gray, 1867; Lyon, 1911; Shelford, 1916; Banks, 1931), as exemplified by Banks' (1949) description of the species “run[ning] off swiftly along the ground, usually obscured by a large, bushy, fox-like tail”. Banks (1949) further noted that tail of *Rheithrosciurus* so obscured the animal in flight, “that it is hard to tell what it looks like and to define”. Abbott (in Lyon, 1911) thought the large bushy tail carried straight out behind gave an impression of an animal at least the size of a large Silvered Leaf Monkey (*Trachypithecus cristatus*), which has a head-body length of up 75 cm compared to 35 cm in *Rheithrosciurus* (Payne *et al.*, 1985).

Speculation on the tail function in *Rheithrosciurus*: Over a number of years, we received 7 camera trap photos of *Rheithrosciurus* (see Fig. 1A–B), which mostly show the tail in an upright or curved position. To assess the size of the tail of *Rheithrosciurus* relative to its body, we estimated the approximate tail volume (i.e., the total volume of the tail bush) as a percentage of body volume. This

indicates an approximate tail volume in *Rheithrosciurus* of 130% relative to body volume. We compared this estimate to other mammal species with large, bushy tails by searching for images of large-tailed mammal species on the internet and in mammal identification guides (Table 1). This analysis suggests that *Rheithrosciurus* has one of the most voluminous tails among all mammals relative to body size. Does this large tail share similar functions with those in other large-tailed mammals (Table 1)?



Figure 1: Camera trap photos of *Rheithrosciurus macrotis* in **A**, Sarawak, Malaysia (Photo: J. Brodie); **B**, lowland Dipterocarp forest in East Kalimantan, Indonesia (Photo: D. Augeri).

Table 1: Tail volume estimates relative to body size in selected mammal species with relatively large tail (TV, tail volume; BV, body volume).

Species	TV/BV (%)	Tail function	Reference
Red Squirrel <i>Sciurus vulgaris</i>	90	To accelerate and steer the squirrel when jumping, keep them balanced, and to keep them warm when they are sleeping.	Muchlinski & Shump, 1979
Giant Ant Eater <i>Myrmecophaga tridactyla</i>	80	Acts as disruptive camouflage, and to conserve body heat especially when sleeping—they are often found sitting in a way so that their tail absorbs heat from the sunlight.	Medri & Mourão, 2005
Red Panda <i>Ailurus fulgens</i>	40	Provides balance and excellent camouflage against its habitat of moss and lichen covered trees.	Pocock, 1941
Ring-tailed Cat <i>Bassariscus astutus</i>	100	Provides balance for negotiating narrow ledges and limbs, even allowing them to reverse directions by performing a cartwheel.	Williams, 2013
Spotted Skunk <i>Spilogale gracilis</i>	35	Acts as a warning to other creatures before it secretes a liquid via paired anal subcutaneous glands.	Kaplan & Mead, 1994
Aye-aye <i>Daubentonia madagascariensis</i>	80	Tail rolled up around body when asleep.	Petter, 1977
Brush-tailed Phascogale <i>Phascogale tapoatafa</i>	90	Can be erected which makes it look larger.	Menkhorst & Knight, 2001
Common Striped Possum <i>Dactylopsila trivirgata</i>	100	The tail is prehensile.	McKay, 1999
Squirrel Glider <i>Petaurus norfolcensis</i>	100	Acts as a rudder when gliding. Also used as another limb as it can curl round branches.	Morcombe & Morcombe, 1974

Maintaining a large bushy tail presumably requires some energetic sacrifice, and there must be good evolutionary reasons to justify the expense. In his seminal review of mammalian tails Hickman (1979) discussed various functions of tails: mechanical functions, including inertia, balance, brake, transportation and construction, and defence; behavioural functions, including autocommunication, warning, courtship, and family and group cohesion; and physiological functions, including thermoregulation, food storage and water balance. Although most other tree squirrels of the tribe Sciurini are arboreal (Thorington *et al.*, 2012), *Rheithrosciurus* is found primarily on the ground or lower tree trunks (Banks, 1931; Payne *et al.*, 1985). A balancing function of the tail for moving along tree branches is therefore not very likely. Mjöberg (1930) speculated that wrapping the bushy tail around its body would keep *Rheithrosciurus* warm in the montane environments where it occurs. Although mostly found in hilly areas (Payne *et al.*, 1985), *Rheithrosciurus* is not restricted to montane environments, as attested by the lowland records along the Kendawangan River and in Pamukan Bay (Lyon, 1911). Night temperatures in such tropical lowland sites would not require protection against the cold, although we cannot exclude the possibility that *Rheithrosciurus* evolved in colder areas and that the tail once had a temperature regulation function. There are no behavioural studies of *Rheithrosciurus*, and possible roles of its tail in autocommunication, warning, or courtship may exist. Another possibility is that the tail has a defence function. *Rheithrosciurus* is the largest of the terrestrial squirrels on Borneo, but the only terrestrial squirrel on the island largely feeding on fruit (but see anecdotal stories below) (Payne *et al.*, 1985). Other terrestrial squirrels, such as Three-striped Ground Squirrel *Lariscus insignis* and Shrew-faced Ground Squirrel *Rhinosciurus laticaudatus*, feed primarily on invertebrates, and these are on average much smaller than *Rheithrosciurus*. The second largest Borneo terrestrial squirrel is Everett's Ground Squirrel *Dremomys everetti*, but it is only 41% of the body size of *Rheithrosciurus* (Payne *et al.*, 1985). The Sciurini to which *Rheithrosciurus* belongs are mostly arboreal frugivores (Thorington *et al.*, 2012). *Rheithrosciurus* thus appears to have maintained the dietary specialization of the Sciurini, but adapted to more terrestrial habits. A relatively large body size and terrestrial habits requires effective defence against terrestrial predators, such as Sunda Clouded Leopard *Neofelis diardi*. It may well be that the very large, fluffy tail of *Rheithrosciurus* is an anti-predator mechanism. In flight, the grey tail, which consists mostly of long fur, obscures the actual body of the animal. This could either confuse a predator in pursuit, or if the predator would pounce on the squirrel it would most likely strike at the tail, which would provide a predator with limited hold. This hypothesis needs to be supported by more detailed behavioural observations before it can be accepted, but it seems the most logical explanation of the *Rheithrosciurus*'s extravagant tail. These considerations might also explain why *Rheithrosciurus* only survives on Borneo. In the Indo-Malayan Realm, Borneo is the island with the least predator species (Meijaard, 2004). Among the mammalian predators on Borneo, probably only Sunda Clouded Leopard *Neofelis diardi*, Bay Cat *Catopuma badia*, or Marbled Cat *Pardofelis marmorata* could predate on *Rheithrosciurus*. In other parts of South East Asia, Leopard *Panthera pardus*, Dhole *Cuon alpinus*, and a range of other carnivores could significantly heighten predation pressure on a terrestrial species. It might well be that a species that was already vulnerable to terrestrial predation only managed to survive where this predation pressure was lowest, i.e., the low mammalian biomass forests of Borneo (Payne, 1990).

***Rheithrosciurus* Folklore:** We admit that much of the above is speculative, but hope that these ideas will stimulate others to pay closer attention to the morphology and behaviour of this unusual squirrel species. A more detailed study of more camera pictures might provide new insights into tail positioning under different conditions (in flight, at rest etc.). It will not be easy to study this uncommon and elusive species on the ground in dense rainforests where direct observation would be much hampered. Some insights may be obtained from talking to local hunters who may have more frequently observed the species, either at rest or in flight when chased by a hunter or his dogs. In fact, there is a relatively rich animal folklore regarding *Rheithrosciurus*. People of Borneo have traditionally hunted the species for meat and ornamental use of its tail, among others to adorn machetes (Banks, 1931). Remarkably for a squirrel, forest-dwelling people consider this squirrel to be quite fierce (J. Payne, pers. comm.). One of us (RD) was in fact told a story by a local hunter in northern Central Kalimantan (Indonesian Borneo) of *Rheithrosciurus* attacking and killing deer to eat the ruminant's stomach contents, liver and heart. On asking how a squirrel could kill a large animal such as a muntjak, *Muntiacus muntjak*, the response was that the squirrel waits on a low branch for a

deer to pass below, jumps on its back and bites the jugular vein, whereon the deer bleeds to death. Once dead the squirrel proceeds to disembowel the deer and eat the stomach contents, heart and liver. Dayak hunters sometimes find these disembowelled deer in the forest, none of the flesh eaten, which to them is a clear sign of a squirrel kill. In villages close to the forest edge there were also accounts of the squirrel killing domestic chickens and eating the heart and liver only. Although, the existence of carnivorous squirrels might be a bit hard to believe, the above might fit the description of Banks (1949), who notes that *Rheithrosciurus* is known as being “wary, difficult to observe and biting fiercely”. Also, other squirrels, such as the Giant Squirrel *Ratufa affinis* are known to actively hunt birds and other vertebrates (R. Ratajszczak, pers. comm.), so we keep an open mind as to what other surprises *Rheithrosciurus* may reveal on further study. After all, another seemingly unlikely hunter story from Borneo of deer of the genus *Tragulus* hiding underwater for long periods of time also turned out to be true (Meijaard *et al.*, 2010). Such finds reiterate how little we know about Bornean wildlife, and *Rheithrosciurus* is only one among many fascinating species on this remarkable island requiring our attention as scientists and conservationists.

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