RAFFLES BULLETIN OF ZOOLOGY **69**: 497–506
Date of publication: 22 November 2021
DOI: 10.26107/RBZ-2021-0067
http://zoobank.org/urn:lsid:zoobank.org:pub:323C1E4F-3A54-47E1-B003-ED6A0CB94FB5

Extreme ecological specialisation in a rainforest mammal, the Bornean tufted ground squirrel, *Rheithrosciurus macrotis* Gray, 1867

Andrew J. Marshall[1*], Erik Meijaard[2] & Mark Leighton[3]

Abstract. The endemic Bornean tufted ground squirrel, *Rheithrosciurus macrotis*, has attracted great interest among biologists and the public recently. Nevertheless, we lack information about the most basic aspects of its biology. Here we present the first empirical data on the feeding ecology of tufted ground squirrels and use data from 81 sympatric mammalian and avian vertebrates to place it within a broad comparative context. *Rheithrosciurus macrotis* is a seed predator and shows much more extreme ecological specialisation than any other vertebrate, feeding on a far smaller subset of available plant foods and demonstrating a greater reliance on a single plant species—*Canarium decumanum*. Our results suggest that *R. macrotis* plays an important, previously unknown role in the ecology of Bornean lowland forests and highlight how much we have yet to learn about the fauna inhabiting some of the most diverse, and most severely threatened, ecosystems on the planet.

Key words. Borneo, *Canarium decumanum*, diet breadth, Indonesia, keystone species, seed predation

INTRODUCTION

The Bornean tufted ground squirrel, *Rheithrosciurus macrotis* Gray, 1867, has been one of the most talked-about squirrels in recent years. This began with its characterisation in the journal *Science* as the ‘vampire squirrel’ (Stokstad, 2014), which followed an account of local folklore that alleged these squirrels kill deer (Meijaard et al., 2014). The moniker ‘vampire squirrel’ spread widely on social media across the globe. Interest in the squirrel spiked again in 2015 with the release of the first video recordings of these squirrels in the wild at Gunung Palung National Park in West Kalimantan (Stokstad, 2015). Despite this global attention, *R. macrotis* remains a very poorly known and largely unstudied species. What we do know is that the species is unusual in many respects. Firstly, phylogenetically it is the only species in Southeast Asia related to the Sciurini (De Waldheim, 1817) tribe, a large group of Holarctic and South American squirrel species. How *R. macrotis* colonised Borneo remains unclear because there are no known fossils that link it with the other Sciurini from which it separated some 8.6 million years ago (Mercer & Roth, 2003; Pečnerová & Martínková, 2012; Pečnerová et al., 2015). *Rheithrosciurus macrotis* also stands out because of its unusual incisors in both the upper and lower jaw, which bear a number of deeply carved ridges (~10) so that the incisors’ cutting edge is saw-shaped (Gray, 1867), an arrangement apparently not recorded among other mammals (Jentink, 1897). Its species name likely links to this feature, with the Greek ‘ρείθρο’ meaning gutter or groove. In addition, comparative morphometric analyses of squirrel mandibles show that *R. macrotis* is a dramatic outlier compared to other squirrels, particularly in its short, robust mandibles with short, wide articular processes (Casanovas-Vilar & van Dam, 2013). Finally, *R. macrotis* appears to have the largest tail relative to body size of all mammal species, a possible anti-predator adaptation (Meijaard et al., 2014).

Although *R. macrotis* is a biogeographic enigma and morphologically unique, little of its basic ecology is known. To our knowledge there has not been any systematic field study of the species’ ecology, although it has been recorded on camera traps at several sites in Borneo (e.g., Mohd-Azlan & Engkamat, 2006; Bernard et al., 2013), where it is endemic. The large size and unusual shape of *R. macrotis* skulls (Zahn, 1941; Casanovas-Vilar & van Dam, 2013) coupled with their extremely stout incisors and powerful masseter muscles (Gyldenstolpe, 1920; Thorington & Darrow, 1996) suggest the species is adapted to feeding on extremely hard seeds (i.e., those with thick, dense seed coats that are highly resistant to deformation; Blate et al., 1998; Lucas et al., 2000), but information on the species’ feeding ecology is lacking. For example, it is unclear to what extent tufted ground squirrels focus on a small number of plant taxa, if their consumption of hard seeds is largely confined to certain periods, or whether their consumption of hard objects is obligate or facultative (sensu Shipley et al., 2009).

Accepted by: Norman Lim T-Lon

[1] Department of Anthropology, Department of Ecology and Evolutionary Biology, Program in the Environment, and School for Environment and Sustainability, 101 West Hall, 1085 S. University Ave, Ann Arbor, Michigan, 48109 USA; Email: ajmarsha@umich.edu (*corresponding author)

[2] Borneo Futures, Block C, Unit C8, Second Floor, Lot 51461, Kg Kota Batu, Mukim Kota Batu, BA 2711, Brunei Darussalam

[3] Harvard University, 11 Divinity Ave, Cambridge, MA, 02138, U.S.A

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

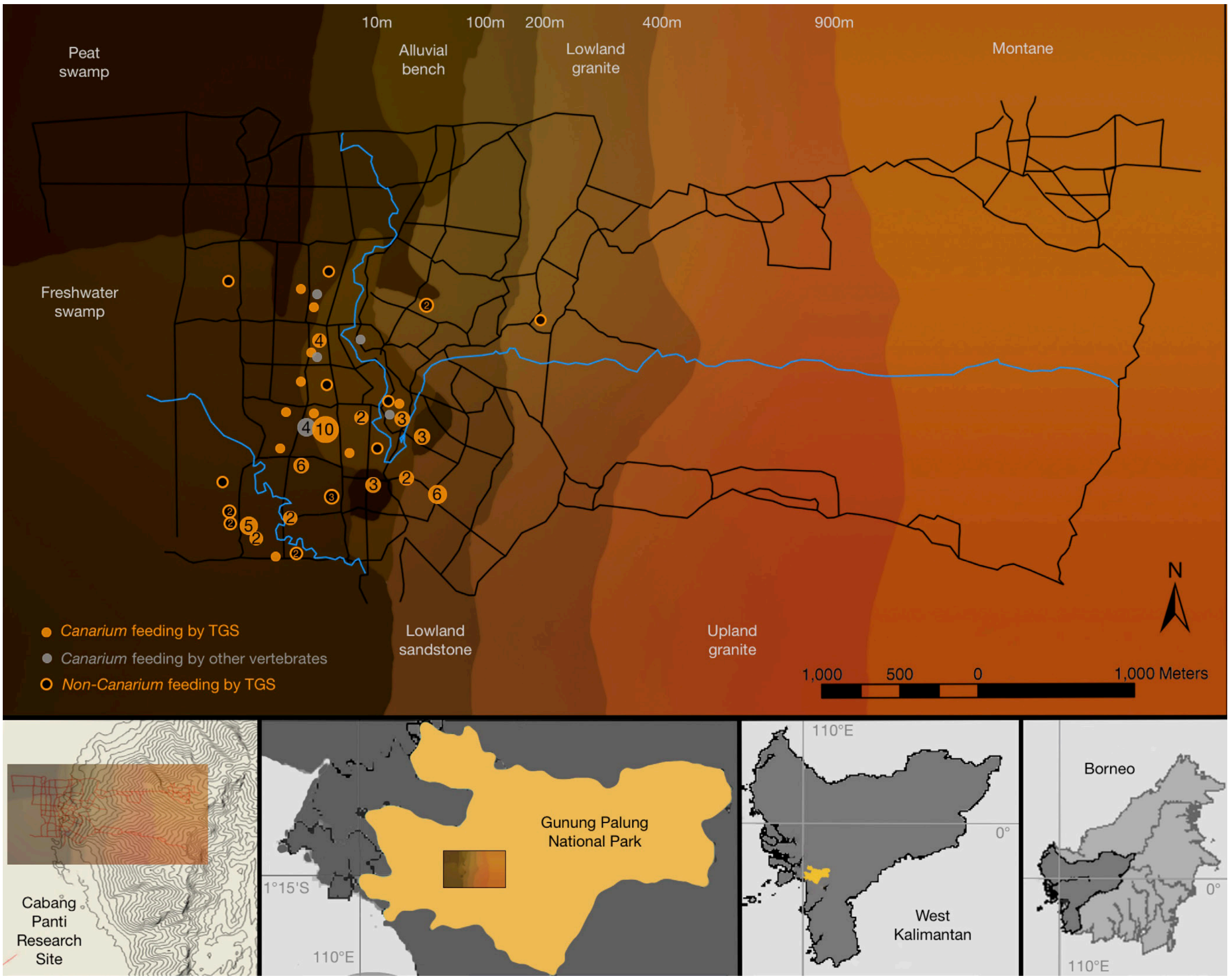

Fig. 1. Study site. Top panel depicts the trail system (black lines) at the Cabang Panti Research Site. Rivers are indicated in blue and the seven forest types are differentiated by colour. The numbers across the top indicate rough elevation (in metres above sea level) of the contour line separating the adjacent forest types (although habitat boundaries only loosely follow elevational contours). Dots indicate observations of *Canarium* feeding by tufted ground squirrels (solid orange) and other vertebrates (solid grey) and feeding on non-*Canarium* plants by tufted ground squirrels (open orange circles). Where multiple feeding observations were made in the same tree, the number of observations is indicated by a number; dots without a number were locations where a single feeding observation was made. The bottom panels show, from left to right, contour lines of the area inside and surrounding the trail system, the location of the study site within Gunung Palung National Park, the park's location in West Kalimantan, and the location of West Kalimantan on Borneo. Figure modified from Marshall et al. (2021).

Here we present long-term, comparative data on the feeding ecology of an intact community of Bornean rainforest vertebrates to describe the diet of *R. macrotis* and place the degree of its ecological specialisation in comparative context. Based on anecdotal published characterisations (Jentink, 1898; Phillipps & Phillipps, 2016), we hypothesised that *R. macrotis* diets would be dominated by fruit of plants containing hard seeds. In addition, we hypothesised that the extreme morphological specialisation of tufted ground squirrels would be reflected in comparatively extreme ecological specialisation on a limited subset of available plants.

MATERIAL AND METHODS

We analysed long-term feeding data gathered at the Cabang Panti Research Site (CPRS) in Gunung Palung National Park, West Kalimantan, Indonesia (1°13′S, 110°70′E, Marshall et al., 2014, 2021; Fig. 1). The dataset was initially gathered as part of a long-term research programme that investigated the ecological processes that maintain biological diversity and collected data relevant to applied problems of rainforest management and conservation. This research entailed, among other things, gathering systematic information on the diets and densities of vertebrate frugivores and monitoring the phenology of plants in botanical plots. Gunung Palung National Park is a formally protected area, and all required permits and approvals were secured for the duration of the study from the Indonesian Institute of Sciences (LIPI), the Directorate General for Nature Conservation (PHKA, now KSDAE), and the Gunung Palung National Park Unit (UTNGP, now BTNGP). The CPRS encompasses roughly 34 km^2 and contains seven tropical forest types, classified based on soil type, drainage, altitude, and parent rock: peat swamp, freshwater swamp, alluvial bench, lowland sandstone, lowland granite, upland granite, and montane (Marshall et al., 2009b; Marshall, 2010). Floristic composition, plant productivity, and mammal densities differ substantially across the habitat gradient (Cannon et al., 2007a, b; Marshall, 2009; Marshall et al., 2014). During the period of data collection, the site was largely unaffected by hunting or illegal logging, suggesting that the vertebrate and plant communities at the site are characteristic of Bornean lowland forests over recent ecological history.

The feeding data used to describe the diets of *R. macrotis* and compare them to other resident vertebrates were collected by ML and colleagues between March 1985 and March 1992. Trained observers recorded all instances of feeding by vertebrates along standardised census routes through the forest and opportunistically during other fieldwork. Census routes were approximately 3.5 km in length and followed small foot trails through the forest. There were two routes in each forest type, and researchers walked each of the routes twice per month (starting at opposite ends) at the same speed and time of day (beginning at 0530 h). In order for an observation to be classified as feeding, an observer had to directly observe an animal placing an item (e.g., leaf, fruit) into its mouth and masticating it; an observation of a species merely handling a potential food item did not constitute a feeding observation. Observers recorded the plant genus on which the animal fed and, when relevant, the ripeness stage of the fruit and the fruit part ingested (see next paragraph). Here we analysed only observations of feeding by vertebrates on fruit or fruit parts (e.g., pulp, seeds), and restricted analyses to independent feeding observations. Thus, we excluded multiple observations made of the same vertebrate species feeding in or under the same tree on the same day and observations made during focal fruit tree watches. This resulted in 4,090 independent feeding observations (see Marshall et al., 2009b for a full description of methods). The data set comprises feeding observations for 82 mammalian and avian taxa. Primates (42% of observations) and Rodentia (19%) were the most well-sampled mammalian orders, with additional observations of Artiodactyla (5%), Carnivora (1.6%), and Chiroptera (1.5%). Bucerotiformes (14%), Passeriformes (7%), and Piciformes (6%) were the best-sampled avian taxa; with additional observations of Columbiformes (1.9%), Galliformes (1.4%), Psittaciformes (0.6%), and Trogoniformes (0.2%).

We assessed plant phenology in 126 plots that were monitored monthly between June 1985 and December 1991 to assess temporal variation in food availability. Plots were either 0.1 or 0.2 ha in size and were placed using a stratified random design across all seven habitat types (for details see Cannon & Leighton, 2004; Marshall & Leighton, 2006). In these plots all trees larger than 14.5 cm dbh, all lianas larger than 3.5 cm dbh, and all hemiepiphytic figs whose roots reached the ground were measured and tagged. The phenological phase of each tagged stem in these phenology plots was recorded each month as one of six mutually exclusive categories: reproductively inactive, or containing flower buds (i.e., developing flowers were visible, but no flowers were at anthesis); mature flowers (i.e., at least one flower on the tree was at anthesis); immature fruit (i.e., fruits in which the seed was undeveloped); mature fruit (i.e., full-sized fruits that were unripe but had seeds that were fully developed and hardened); or ripe fruit (i.e., at least one fruit on the tree was ripe, usually signalled by a change in colour or softness). We calculated the proportion of monitored stems with mature or ripe fruit in each month as an index of fruit availability for vertebrates. We also calculated this value for the *Canarium* trees in our phenology plots (n = 14 stems total). To examine whether feeding observations were related to fruit availability, we built simple linear models with the number of feeding observations per month as the dependent variable and the proportion of stems with mature or ripe fruit per month as the independent variable and report adjusted R^2 values.

We assessed the ecological specialisation of all vertebrates in our dataset by comparing the observed dietary diversity for each taxon to their predicted dietary diversity. To do this, we plotted plant genus accumulation curves for all vertebrates and used the species-specific residuals as our index of specialisation. We considered vertebrates with large negative residual values to be highly specialised because they fed on a smaller number of plant genera than was expected based on the number of feeding observations made. We used plant genera as the unit for our comparative analyses to account for different levels of taxonomic certainty among plant groups at CPRS (Bacci et al., 2009; Timms et al., 2013; Dillis et al., 2015).

To compare the extent of specialisation on specific plant genera, we analysed the dietary composition of all vertebrates for which at least 70 independent feeding observations were available (mean = 274 observations, range 72–549). This sample size was a natural break point in the data and resulted in a sample of 12 well-sampled species for comparative analysis. We used the program R 4.1.0 for all analyses (calculation of genus accumulation curves, ordinary least-squares regression, and coefficients of variation) and to produce the figures (R Core Team, 2021). We used the R packages dplyr 1.0.7 (Wickham et al., 2021) and lubridate 1.7.10 (Grolemund & Wickham, 2011) to summarise data; all other work was done in base R.

RESULTS

The field team recorded a total of 79 independent feeding observations for *R. macrotis*, somewhat more than for the typical taxon in our dataset (mean = 52, SD = 112, range 1–549 observations/species). The majority of tufted ground squirrel feeding observations (n = 60; 76%) were made during vertebrate censuses; the remaining were made as researchers were conducting other fieldwork (n = 19, 24%). Feeding observations of *R. macrotis* were spread across the

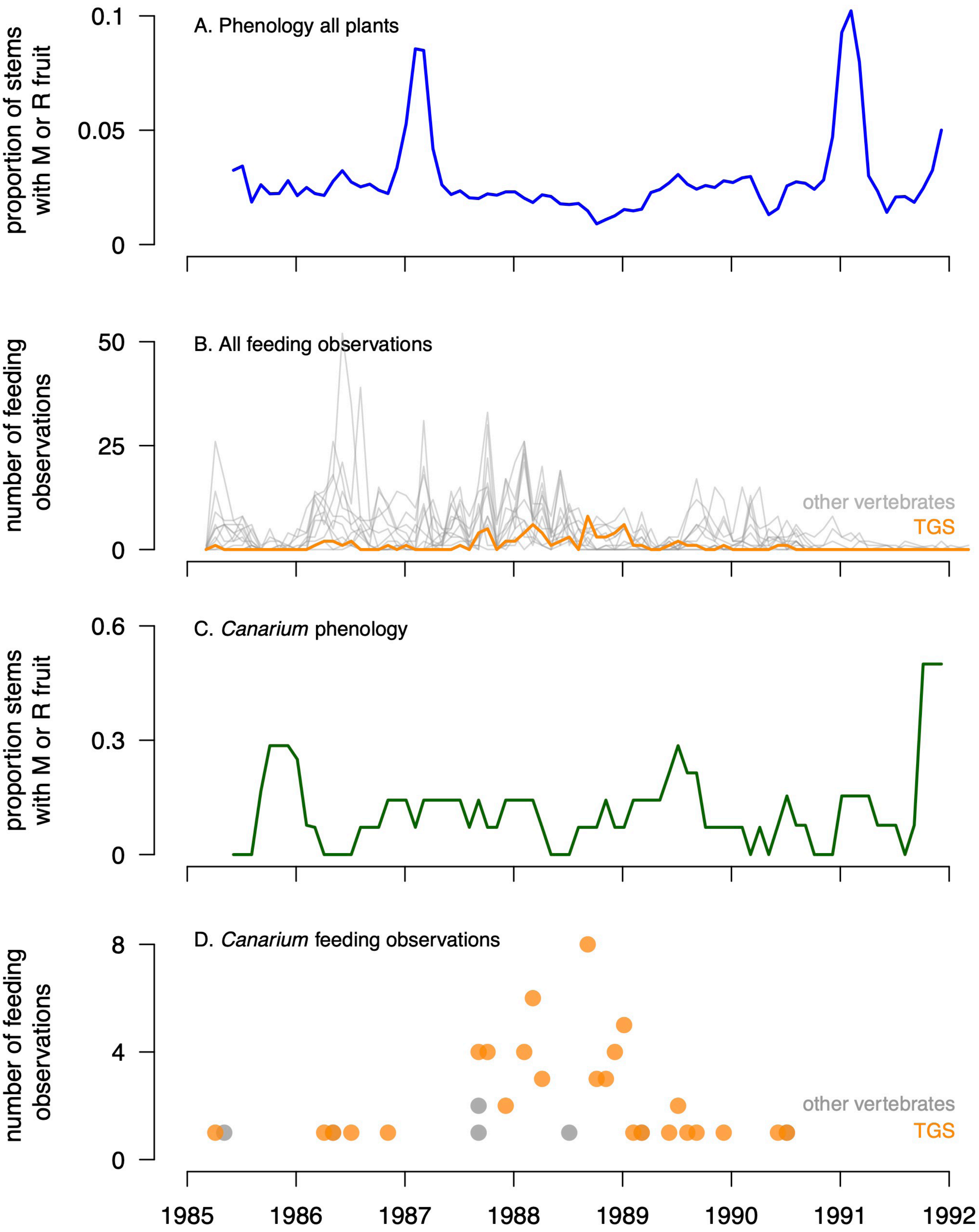

Fig. 2. Plant phenological patterns and temporal distribution of feeding observations. A. The proportion of monitored plants in our 126 phenology plots bearing mature or ripe fruit in each month. B. The temporal distribution of feeding observations made of tufted ground squirrels (TGS, orange line) and the eleven other most well-sampled vertebrates (grey lines). C. The proportion of all *Canarium* stems in our phenology plots (n = 14) bearing mature or ripe fruits in each month. D. The temporal distribution of *Canarium* feeding observations made of tufted ground squirrels (TGS, orange dots) and the eleven other most well-sampled vertebrates (grey dots).

five lowland forest types, but were most common in the freshwater swamp, alluvial bench, and lowland sandstone forests (Fig. 1), the forest types where the tufted ground squirrel was most encountered (whether it was feeding or not). Observations of tufted ground squirrel feeding were spread fairly evenly across the sampling period (Fig. 2B) and were not closely related to overall patterns of plant phenology at the site (Fig. 2A, $R^2 = 0.08$). The temporal distribution of *R. macrotis* feeding observations was comparable to that of the other 11 most well-sampled vertebrates (Fig. 2B). The coefficient of variation in the number of monthly feeding observations for tufted ground squirrels (CV = 1.69) was well within the range of the 11 other well-sampled species (CV range: 0.90–3.93) and close to their mean value ($CV_{mean} = 1.74$).

The 79 feeding records for tufted ground squirrels documented consumption of five plant taxa; the average number of plant genera recorded for each vertebrate taxon was ten (SD = 19, range = 1–88). The most commonly observed taxon in the *R. macrotis* diet was *Canarium decumanum* (n = 61 observations, 77%), followed by *Mezzetia leptopoda* (n = 10, 13%), *Elaeocarpus* spp. (n = 4, 5%), *Dracontomelon dao* (n = 3, 4%), and *Irvingia malayana* (n = 1, 1%). Tufted ground squirrels consumed *Canarium* in six of the seven years over which the study was conducted (Fig. 2D). Their consumption of *Canarium* seeds was not strongly related to *Canarium* fruit availability (Fig. 2C, $R^2 = –0.01$) or general patterns of forest fruit availability (Fig. 2A, $R^2 = 0.06$), although we note that no observations of *Canarium* feeding were made during either of the mast fruiting events that occurred during the sampling period (the two high peaks in Fig. 2A). All *R. macrotis* feeding observations entailed feeding on seeds below or near fruiting *Canarium* trees. Although comparative empirical data on seed hardness are not available for all of the species on which the tufted ground squirrel was observed to feed, seeds in the genera *Canarium* and *Eleaocarpus* were the hardest of those measured at Gunung Palung (Blate et al., 1998) and *Canarium* and *Mezzetia* are widely known to be among the hardest seeds found in the Bornean rainforest (AJM, ML, personal observations; Vogel et al., 2008; Lucas et al., 2012). Thus, as we hypothesised, the diet of *R. macrotis* is dominated by a small number of plant taxa with extremely hard seeds. Indeed, the plant taxa fed upon by tufted ground squirrels are rarely consumed by any other vertebrates, presumably because their hard seeds are inaccessible to most other taxa (Blate et al., 1998). For example, of the 69 independent feeding observations of *Canarium* seeds, 61 (88%) were by *R. macrotis* (Fig. 2D). The only other taxa we observed eating *Canarium* seeds were bearded pigs (*Sus barbatus*) and giant squirrels (*Ratufa affinis*), each of which were observed to feed on them four times (6%). Of the 15 observations of vertebrate feeding on *Mezzetia* seeds, ten (67%) were by *R. macrotis* and the remaining five were by bearded pigs (*Sus barbatus*, n = 3, 20%) and giant squirrels (*Ratufa affinis*, n = 2, 13%).

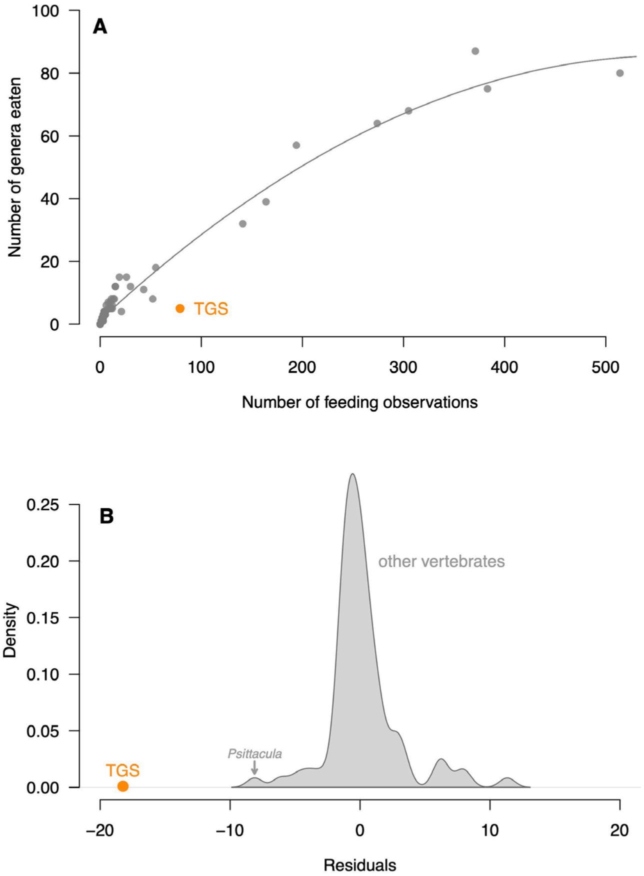

Fig. 3. Taxonomic richness of vertebrate frugivore diets. A. Plot shows the number of plant genera consumed by each vertebrate species plotted against sample size. The curve shows predicted dietary richness. B. The distribution of species-specific residuals from the curve in panel A. Both plots show that the tufted ground squirrel (TGS, indicated in orange) consumes a much more restricted number of plant genera than expected and exhibits a much more negative residual than any other taxon.

We also found support for our second hypothesis. *Rheithrosciurus macrotis* was extremely ecologically specialised, restricting its feeding to a smaller subset of plant genera than any other vertebrate taxon in our dataset. We observed vertebrate feeding on 159 plant genera. As expected, the number of plant genera recorded in a vertebrate species' diet increased in a decelerating curvilinear fashion with the number of feeding observations recorded (Fig. 3A, $R^2 = 0.97$, n = 82 vertebrates, $p < 0.001$). Species-specific residuals from this curve (our measure of ecological specialisation) ranged from –18.3 to 11.3 (Fig. 3B). Birds were slightly more specialised than mammals (bird mean residual = –0.182, range = –8.12 to 6.11; mammal mean residual = 0.31, range = –18.2 to 11.3), but class was not a reliable predictor of specialisation; in a linear model using class to predict specialisation the 95% CI of β_{mammal} ranged from –1.1 to 2.1 ($R^2 = –0.01$, $p = 0.54$). *Rheithrosciurus macrotis* exhibited a residual value of –18.3, indicating that it was recorded feeding on 18 fewer plant genera than predicted based on the number of feeding observations made. No other taxon exhibited such specialisation; the range of residuals for other species ranged from –8.1 to 11.3 (Fig. 3B). The closest species to *R. macrotis* was the long-tailed parakeet (*Psittacula longicauda*; residual = –8.1), which is also a highly specialised seed predator (Curran & Leighton, 2000).

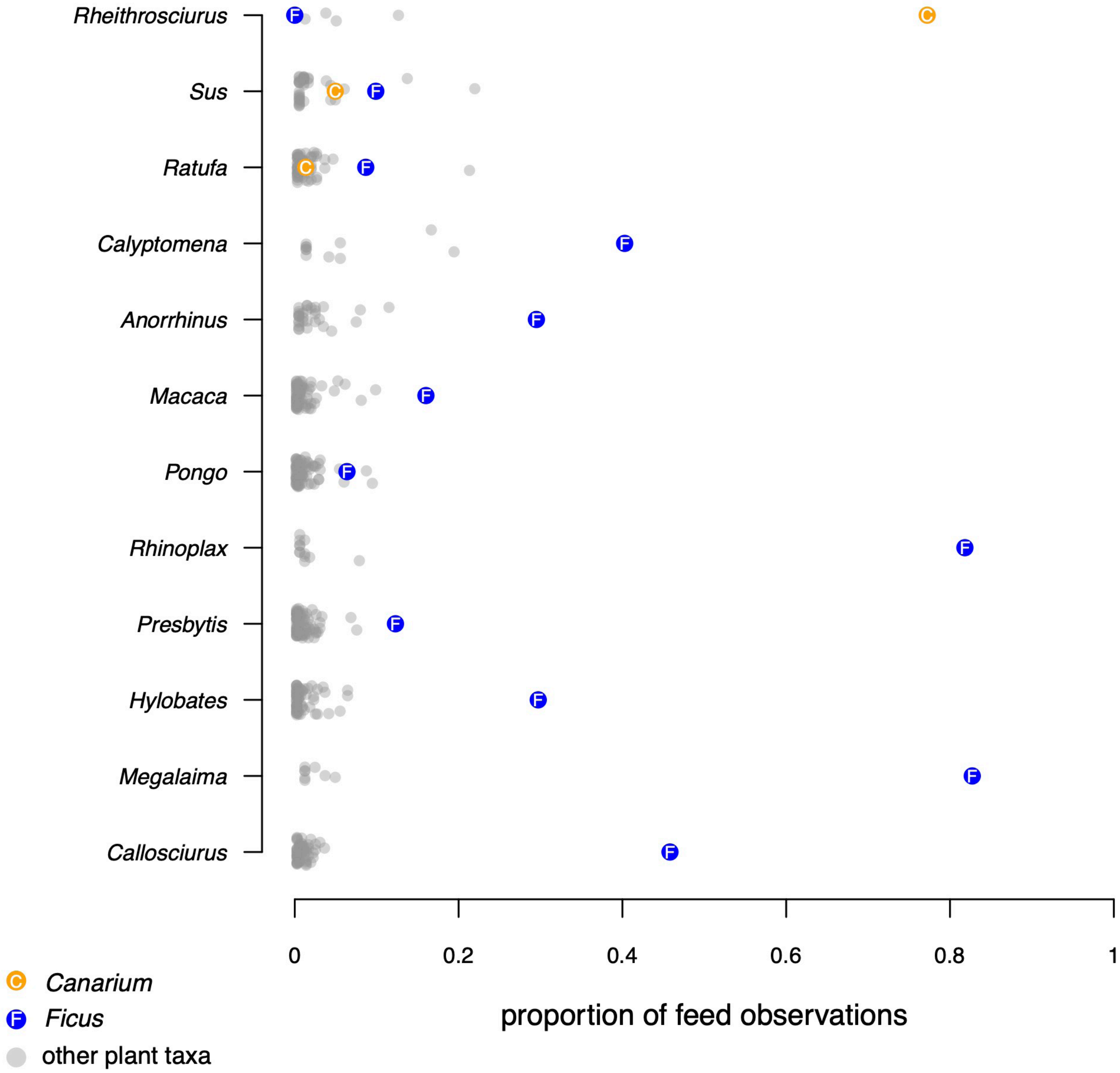

Fig. 4. Ecological specialisation among the 12 most well-sampled vertebrates at our study site. Each dot represents the dietary importance (proportion of total feeding observations) of a plant genus fed upon by the indicated vertebrate taxon. Orange and blue dots indicate the importance of *Canarium* and *Ficus*, respectively; all other plant taxa are depicted with grey dots. Vertebrate species are listed in decreasing order from the top, based on the importance of the most important non-fig plant genus in the diet: *Rheithrosciurus macrotis*, *Sus barbatus*, *Ratufa affinis*, *Calyptomena viridis*, *Anorrhinus galeritus*, *Macaca fascicularis*, *Pongo pygmaeus*, *Rhinoplax vigil*, *Presbytis rubicunda*, *Hylobates albibarbis*, *Megalaima chrysopogon*, and *Callosciurus prevostii*.

We repeated our analyses using mammalian data only and the results were similar (residual for *R. macrotis* = –19.1, range for other species was –5.6 to 10.7). In our analysis using mammals only, squirrels appeared to be somewhat more specialised than other mammals (mean residual squirrels = –0.85, mean other mammals = 0.31), but this effect was driven entirely by the tufted ground squirrel. When we excluded its residual from the comparison, squirrels were substantially less specialised than other mammals (mean residual squirrels = 1.75, mean residual other mammals = 0.31). To examine whether our results were driven by combining observations of seed predation with other instances of frugivory, we repeated our analysis using only observations of seed eating in the full dataset (n = 802 observations, 25 vertebrate species). The tufted ground squirrel again had the smallest residual (–18.4). The only other species with large negative residuals were orangutans (*Pongo pygmaeus*, residual = –13.6) and, as above, long-tailed parakeets (residual = –9.5). We note that while the seed portion of the orangutan's diet indicates substantial specialisation, seed eating comprised a small subset of orangutan feeding observations (n = 27%, 149 of 549 observations), while all tufted ground squirrels feeding observations were on seeds.

To further examine the extent of dietary specialisation of tufted ground squirrels relative to sympatric vertebrate frugivores, we calculated the importance of each plant taxon in the diets of the twelve most well-sampled vertebrates at CPRS. *Canarium* comprised 77% of all *R. macrotis* feeding observations. Only the diverse, keystone plant genus *Ficus* was comparable in its importance in vertebrate diets, comprising more than 80% of the diets of rhinoceros hornbills (*Rhinoplax vigil*) and gold-whiskered barbets (*Megalaima chrysopogon*) and more than 20% of the diets of four other frugivores (Fig. 4). No other plant genus constituted more than 22% of the feeding observations of our 12 most well-sampled vertebrate taxa. Interestingly, after *R. macrotis*, the two vertebrates with the largest reliance on a non-fig plant genus were the seed predators bearded pigs (for which *Shorea* seeds constituted 21.9% of feeding observations) and giant squirrels (for which *Lithocarpus* nuts constituted 21.3% of feeding observations). Excluding the extremely specialised tufted ground squirrel, the degree of specialisation (i.e., residual value from the genus accumulation curve in Fig. 3) on non-fig items was not well predicted by overall sample size ($\beta = -0.0001$, $R^2 = 0.11$, n = 11 vertebrates, p = 0.33) nor the number of items recorded in the diet ($\beta = -0.0003$, $R^2 = 0.02$, n = 11 vertebrates, p = 0.68).

DISCUSSION

Our systematic data on the feeding ecology of Bornean tufted ground squirrels confirms previous anecdotal descriptions of the species (Jentink, 1898; Phillipps & Phillipps, 2016). We provide clear evidence that the species is a seed predator and focuses its feeding on plants bearing extremely hard seeds, especially *Canarium decumanum* and *Mezzetia leptopoda*. Two measures indicate that *R. macrotis* is the most specialised vertebrate taxon in this forest. First, when we controlled for sampling effort, the taxonomic richness of *R. macrotis* diets is far less than that of any other vertebrate frugivore at Cabang Panti (Fig. 3A, B). These results are consistent whether comparisons are based on all feeding observations by all vertebrates in our data set or are restricted to only mammals, only squirrels, or only observations of feeding on seeds. Second, tufted ground squirrels focus on a single plant genus, *Canarium*, far more than any other vertebrate focuses on a single plant genus, with the exception of feeding on the diverse genus *Ficus* (see below). In this context, it is interesting that one of the first descriptions of *R. macrotis* explains that an individual was "[s]hot in the deep jungle during the morning after heavy rainfall, when the animal was looking for fruit under a *Canarium* tree…" (Jentink, 1898: 125, translated from German).

We characterise the specialisation documented in *R. macrotis* as "extreme" or "intense" based on the magnitude of its residual from the genus accumulation curve (Fig. 3B); it feeds on a far smaller subset of available genera than any other taxon documented in our forest. We are confident that this characterisation is not the result of biased sampling that is restricted in space (Fig. 1) or time (Fig. 2B, D). There remain, however, key aspects of the tufted ground squirrel's feeding ecology that require characterisation before firm conclusions about the ecological significance of their specialisation can be drawn. For example, without comprehensive understanding of the tufted ground squirrel's ability to detoxify plant secondary compounds, or the distribution of these compounds in plant items they consume and ignore, we cannot accurately describe all aspects of their realised, much less their fundamental, niche (Shipley et al., 2009). Similarly, as our data are all observational and collected under natural conditions, we cannot assess to what extent they might be able to expand their diets under different environmental conditions or at different sites.

Nevertheless, our study does provide several key insights into the nature of its specialisation. First, tufted ground squirrels consume highly specialised diets (i.e., they have very narrow realised niches), and their degree of specialisation is far greater than other vertebrate species in our comparative sample. Second, items on which we observed them feeding are not common in the forest, indicating that their specialisation is the result of preference for a specialised subset of available plants. The two plants that constituted 90% of observed feeding observations by tufted ground squirrels (*Canarium decumanum* and *Mezzetia leptopoda*, combined 71 of 79 observations) were only 0.21% (n = 14) and 0.24% (n = 16) of the 6,591 plant stems recorded in our botanical plots. Third, consumption of *Canarium* was not restricted to a small subset of the sampling period (Fig. 2D), indicating that their specialisation is not confined to certain seasons. Fourth, their consumption of *Canarium* is not related to the overall phenological patterns in the forest, suggesting it is not a facultative response to reduce dietary overlap with potential competitors during periods of overall food scarcity (Robinson & Wilson, 1998). These results, combined with indications that the hard seeds on which *R. macrotis* specialises are difficult to process and that their dental specialisation allows them to access these items that are likely unavailable to many other vertebrates (Blate et al., 1998), indicates that they might best be characterised as "obligate specialists" (sensu Shipley et al., 2009). We note, however, that at present we have no evidence that the dental adaptations that permit tufted ground squirrels to feed on very hard seeds impose a cost on their ability to process other available items, thereby restricting their fundamental niches.

Specialised seed predators play crucial functions in the ecology of Southeast Asian rainforests (Janzen, 1974; Blate et al., 1998; Curran & Leighton, 2000). Most commonly discussed are *Psittacula*, *Sus*, and *Ratufa*, which are the taxa in our analysis most similar to *R. macrotis* in their degree of specialisation (*Psittacula*, Fig. 3B) and the magnitude of the importance of a non-fig plant taxon in their diets (*Sus* and *Ratufa*, Fig. 4). The intense specialisation of tufted ground squirrels raises the possibility that they may play an important, heretofore unidentified, role in the ecology of Bornean *Canarium* trees—primarily as a seed predator, although likely as an occasional disperser as well in instances where the squirrel buries a seed and fails to return to feed on it (ML, AJM, personal observations; Phillipps & Phillipps, 2016). Focused seed fate trials at Gunung Palung demonstrated that large, hard *Canarium* seeds were avoided by virtually all seed predators other than *R. macrotis* (Blate et al., 1998). Camera trapping work at our site conducted between 2015 and 2020, including focal camera placement below *Canarium* trees (Marshall, Wittmer & Setiawan, unpublished data; Nelaballi, unpublished data), confirms that *R. macrotis* is the species most commonly seen feeding on *Canarium* seeds. Despite these intriguing indications, the importance of tufted ground squirrel predation on *Canarium* ecology remains to be determined. Trials on isolated seeds at our site suggest that *Canarium* is subject to much lower levels of seed predator-based mortality than other taxa (Blate et al., 1998), a result Blate et al. (1998) hypothesise may be due to the relatively low abundances of the specialised tufted ground squirrel. It is unclear, however, to what extent their results mirror those that might be found using naturally occurring seed shadows. Long-term observations and camera trapping work at Gunung Palung suggest it is very rare to observe a tufted ground squirrel anywhere other than beneath a fruiting *Canarium* tree. Moreover, it is unusual to approach a fruiting *Canarium* tree and not observe a tufted ground squirrel or unambiguous evidence of one having fed there. Results from other sites suggest that rodent seed predators can have important effects on *Canarium* species. For example, in a moist evergreen forest in Thailand, three seed eating and caching rodents (*Leopoldamys sabanus*, *Menetes berdmorei*, and *Maxomys surifer*) heavily predated *Canarium euphyllum* seeds (Kitamura et al., 2008). Similarly, Yasuda et al. (2005) reported that large numbers of *Canarium littorale* seeds were removed by three rodents (*L. sabanus*, *L. insignis*, and *Maxomys* spp.) in Peninsular Malaysia. Our results suggest that the Bornean endemic *R. macrotis* has a strong effect on the seed shadows of *Canarium decumanum* trees on this island. If so, the effect of tufted ground squirrels on *Canarium* ecology likely has cascading effects on other large canopy tree species that compete with *Canarium*. For example, in the absence of seed predation by *R. macrotis*, *Canarium* might reach considerably higher densities, at the detriment of competing species. Further work will be required to further examine these possibilities.

Ficus is the one plant taxon that exceeds *Canarium* in its importance in the diets of frugivores at the Cabang Panti Research Site (Fig. 4). This is not unexpected, both because *Ficus* is a highly diverse plant taxon at this site (n = 56 species in Gunung Palung National Park; Laman & Weiblen, 1998) and because it exhibits phenological patterns that make it a keystone species that provides sustenance to a wide range of animals during periods of resource scarcity (Shanahan et al., 2001; Marshall et al., 2009a; Dillis et al., 2015). Moreover, *Ficus* is widely recognised as a uniquely important plant taxon for tropical frugivores, a role it clearly plays at our site: *Ficus* comprises more than 20% of feeding observations for six of our most well-sampled vertebrates (Fig. 4). No other plant genus attains this level of importance in the diet of a vertebrate at our site, with the exception of the importance of *Canarium* seeds for *R. macrotis*. In contrast to the widespread importance of *Ficus*, however, *Canarium* is not of major importance to any other vertebrate taxon, suggesting the intensive use of its seeds by tufted ground squirrels is a uniquely tightly integrated ecological relationship that deserves further investigation. In this regard it is notable that the evolutionary origin and dispersal of *Canarium* bears striking similarities to the tufted ground squirrel. Although the evolutionary history of *Canarium* is incompletely understood, it appears to have initially evolved in North America, subsequently spread across Eurasia and Africa, then later dispersed to the Southern hemisphere (Han et al., 2018), a pattern that is similar to that hypothesised for *R. macrotis* (Pečnerová & Martínková, 2012). Unlike *R. macrotis*, *C. decumanum* is not a Bornean endemic, but is restricted to Borneo, the Moluccas, and New Guinea (LaFrankie, 2010) and it is possible that the extent of its current distribution reflects fairly recent movement by people (Maloney, 1996).

While our data present an intriguing story of intense ecological specialisation in a rainforest mammal, it is notable that 79 feeding observations constitute the most complete account of *R. macrotis* ecology ever published. The tufted ground squirrel has attracted an astonishing amount of interest in the scientific and popular press. Erik Stokstad's news piece on the 'vampire squirrel' was the second-most read and commented upon article on the website of the journal *Science* during the first week of September 2015. *Rheithrosciurus macrotis* also possesses several highly unusual features that make it a legitimate subject of serious research attention. In this context, it is truly remarkable how little we know about the species—although our evidence suggests that "assassin squirrel" would be a better moniker than "vampire squirrel", reflecting its intensive seed predation. This highlights our more general ignorance of the biodiversity of Borneo and other parts of the tropics. The vast majority of published research concerns a very limited subset of taxa (e.g., Brodie, 2009; Marshall et al., 2016), and with forests in Indonesia and across the tropics being lost at alarming rates (FAO & JRC, 2012; Gaveau et al., 2014), we run the risk of losing species before we can collect even the most basic information about their ecology. This is of particular concern for species, such as *R. macrotis*, that are restricted to undisturbed lowland forests and predicted to be highly intolerant of logging and other forms of disturbance (Meijaard & Sheil, 2008).

ACKNOWLEDGEMENTS

We thank associate editor Norman Lim and an anonymous reviewer for constructive comments that improved this paper. Permission to conduct research at Gunung Palung National Park was kindly granted by the Indonesian Institute of Sciences (LIPI), the Directorate General for Nature Conservation (PHKA, now KSDAE), and the Gunung Palung National Park Office (UTNGP, now BTNGP). We are grateful to Universitas Tanjungpura for counterpart support. Data collection was supported by grants to ML from the National Science Foundation (BNS–840–9299), National Geographic Society, the Conservation, Food and Health Foundation, and Merck. We appreciate the assistance and support of the many students, researchers, and field assistants who worked at Cabang Panti Research Site over the past three decades.

Special thanks to Emilio Bruna for suggesting the name "assassin squirrel" and to Swapna Nelaballi for beneficial discussion and sharing her insights into tufted ground squirrel feeding ecology. Contributions: A.J.M. and E.M. conceived of and designed the study, M.L. funded and oversaw field data collection, A.J.M. analysed the data and produced the figures, A.J.M and E.M. wrote the manuscript.

LITERATURE CITED

Bacci T, Trabucco B, Marzialetti S, Marusso V, Lomiri S, Vani D & Lamberti CV (2009) Taxonomic sufficiency in two case studies: where does it work better? Marine Ecology, 30: 13–19.

Bernard H, Ahmad AH, Brodie J, Giordano AJ, Lakim M, Amat R, Hue SK, Khee LS, Tuuga A, Malim PT & Lim-Hasegawa D (2013) Camera-Trapping survey of mammals in and around Imbak Canyon Conservation Area in Sabah Malaysian Borneo. Raffles Bulletin of Zoology, 61: 861–870.

Blate GM, Peart DR & Leighton M (1998) Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. Oikos, 82: 522–538.

Brodie JF (2009) Is research effort allocated efficiently for conservation? Felidae as a global case study. Biodiversity Conservation, 18: 2927–2939.

Cannon CH & Leighton M (2004) Tree species distributions across five habitats in a Bornean rain forest. Journal of Vegetation Science, 15: 257–66.

Cannon CH, Curran LM, Marshall AJ & Leighton M (2007a) Beyond mast-fruiting events: Community asynchrony and individual dormancy dominate woody plant reproductive behavior across seven Bornean forest types. Current Science, 93: 1558–1566.

Cannon CH, Curran LM, Marshall AJ & Leighton M (2007b) Long-term reproductive behavior of woody plants across seven Bornean forest types in the Gunung Palung National Park, Indonesia: suprannual synchrony, temporal productivity, and fruiting diversity. Ecology Letters, 93: 956–969.

Casanovas-Vilar I & van Dam J (2013) Conservatism and adaptability during squirrel radiation: what is mandible shape telling us? PloS One, 8: e61298.

Curran LM & Leighton M (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. Ecological Monographs, 70: 101–128.

Dillis C, Beaudrot L, Feilen KL, Clink DJ, Wittmer HU & Marshall AJ (2015) Modeling the ecological and phenological predictors of fruit consumption by gibbons (*Hylobates albibarbis*). Biotropica, 47: 85–93.

FAO & JRC (2012) Global forest land-use change 1990–2005. FAO Forestry Paper No. 169. Food and Agriculture Organization of the United Nations, Rome; European Commission Joint Research Centre, xi + 40 pp.

Gaveau DL, Sloan S, Molidena E, Yaen H, Sheil D, Abram NK, Ancrenaz M, Nasi R, Quinones M, Wielaard N, & Meijaard E (2014) Four decades of forest persistence, clearance and logging on Borneo. PLoS One, 9: 11.

Gray JE (1867) XXXV.—Synopsis of the Asiatic Squirrels (Sciuridae) in the collection of the British Museum, describing one new genus and some new species. Journal of Natural History Series 3, 20: 270–286.

Grolemund G & Wickham H (2011) Dates and Times Made Easy with lubridate. Journal of Statistical Software, 40(3): 1–25. https://www.jstatsoft.org/v40/i03/ (Accessed 06 October 2021).

Gyldenstolpe N (1920) On a collection of mammals made in eastern and central Borneo by Mr. Carl Lumholtz. Kongliga Svenska vetenskapsakademiens handlingar, 60: 1–62.

Han M, Manchester SR, Wu Y, Jin J & Quan C (2018) Fossil fruits of *Canarium* (Burseraceae) from Eastern Asia and their implications for phytogeographical history. Journal of Systematic Palaeontology, 16: 841852.

Janzen DH (1974) Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. Biotropica, 4: 69–103.

Jentink DFA (1897) Note II. Zoological results of the Dutch scientific expedition to Central Borneo. The Mammals. Notes from the Leyden Museum, 19: 26–66.

Jentink DFA (1898) Note XX. Zoological results of the Dutch scientific expedition to Central Borneo. The Mammals. Notes Leyden Museum, 20:113–125.

Kitamura S, Yumoto T, Poonswad P, Suzuki S & Wohandee P (2008) Rare seed-predating mammals determine seed fate of *Canarium euphyllum*, a large-seeded tree species in a moist evergreen forest, Thailand. Ecological Research, 23: 169–177.

LaFrankie JV (2010) Tree of Tropical Asia: An Illustrated Guide to Diversity. Black Tree Publications, Philippines, 748 pp.

Laman TG & Weiblen GD (1998) Figs of Gunung Palung National Park (West Kalimantan, Indonesia). Tropical Biodiversity, 5: 245–297.

Lucas PW, Gaskins JT, Lowrey TK, Harrison ME, Morrogh-Bernard H, Cheyne SM & Begley MR (2012) Evolutionary optimization of material properties of a tropical seed. Journal of the Royal Society Interface, 9: 34e42.

Lucas PW, Turner IM, Dominy NJ & Yamashita N (2000) Mechanical defences to herbivory. Annals of Botany, 86: 913–920.

Maloney BK (1996) *Canarium* in the Southeast Asian and Oceanic archaeobotanical and pollen records. Antiquity, 70: 926–933.

Marshall AJ (2009) Are montane forests demographic sinks for Bornean white-bearded gibbons? Biotropica, 41: 257–267.

Marshall AJ (2010) Effects of habitat quality on primate populations in Kalimantan: gibbons and leaf monkeys as case studies. In: Supriatna J & Gursky SL (eds.) Indonesian Primates. Springer, New York, pp. 157–177.

Marshall AJ, Beaudrot L & Wittmer HU (2014) Responses of primates and other frugivorous vertebrates to plant resource variability over space and time at Gunung Palung National Park. International Journal of Primatology, 35: 1178–1201.

Marshall AJ, Boyko CM, Feilen KL, Boyko RH & Leighton M (2009a) Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology, 140: 603–614.

Marshall AJ, Cannon CH & Leighton M (2009b) Competition and niche overlap between gibbons (*Hylobates albibarbis*) and other frugivorous vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia. In: Lappan S & Whittaker DJ (eds.) The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology. Springer, New York, pp. 161–188.

Marshall AJ, Farr MT, Beaudrot L, Zipkin EF, Feilen KL, Bell LG, Setiawan E, Susanto TW, Mitra Setia T, Leighton M & Wittmer HU (2021) Biotic and abiotic drivers of dispersion dynamics in a large-bodied tropical vertebrate, the Western Bornean orangutan. Oecologia, 196: 707–721.

Marshall AJ & Leighton M (2006) How does food availability limit the population density of white-bearded gibbons? In: Hohmann G, Robbins MM & Boesch C (eds.) Feeding Ecology of the Apes and other Primates. Cambridge University Press, Cambridge, pp. 311–333.

Marshall AJ, Meijaard E, Van Cleave E & Sheil D (2016) Charisma counts: the presence of great apes affects the allocation of research effort in the paleotropics. Frontiers in Ecology and the Environment, 14: 13–19.

Meijaard E & Sheil D (2008) The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: observations, overviews and opportunities. Ecological Research, 23: 21–34.

Meijaard EM, Dennis R & Meijaard E (2014) Tall tales of a tropical squirrel. Taprobanica, 6: 27–31.

Mercer JM & Roth VL (2003) The effects of Cenozoic global change on squirrel phylogeny. Science, 299: 1568–1572.

Mohd-Azlan J & Engkamat L (2006) Camera trapping and conservation in Lambir Hills National Park, Sarawak. Raffles Bulletin of Zoology, 54(2): 469–475.

Pečnerová P & Martínková N (2012) Evolutionary history of tree squirrels (Rodentia, Sciurini) based on multilocus phylogeny reconstruction. Zoologica Scripta, 4: 211–219.

Pečnerová P, Moravec JC & Martínková N (2015) A skull might lie: modeling ancestral ranges and diet from genes and shape of tree squirrels. Systematic Biology, 64: 1074–1088.

Phillipps Q & Phillipps K (2016) Phillipps' Field Guide to the Mammals of Borneo and Their Ecology. Princeton University Press, Princeton, New Jersey, 400 pp.

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (Accessed 20 May 2021).

Robinson BW & Wilson DS (1998) Optimal foraging, specialization, and a solution to Liem's Paradox. American Naturalist, 151: 223–35.

Shanahan MS, So S, Compton SG & Corlett R (2001) Fig-eating by vertebrate frugivores: a global review. Biological Reviews, 76: 529–572.

Shipley LA, Forbey JS & Moore BD (2009) Revisiting the dietary niche: When is a mammalian herbivore a specialist? Integrative and Comparative Biology, 49: 274–290.

Stokstad E (2014) 'Vampire' squirrel has world's fluffiest tail. Science. http://news.sciencemag.org/plants-animals/2014/06/vampire-squirrel-has-worlds-fluffiest-tail (Accessed 06 July 2014).

Stokstad E (2015) 'Vampire' squirrel caught on film. Science. http://news.sciencemag.org/plants-animals/2015/09/vampire-squirrel-caught-film (Accessed 02 September 2015).

Thorington JRW & Darrow DK (1996) Jaw muscles of Old World squirrels. Journal of Morphology, 230: 145–165.

Timms LL, Bowden JJ, Summerville KS & Buddle CM (2013) Does species level resolution matter? Taxonomic sufficiency in terrestrial arthroapod biodiversity studies. Insect Conservation and Diversity, 6: 453–462.

Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP & Dominy NJ (2008) Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. Journal of Human Evolution, 55: 60–74.

Wickham H, François R, Henry L & Müller K (2021) dplyr: A Grammar of Data Manipulation. R package version 1.0.7. https://CRAN.R-project.org/package=dplyr (Accessed 06 October 2021).

Yasuda M, Miura S, Ishii N, Okuda T & Hussein NA (2005) Fallen fruits and terrestrial vertebrate frugivores: a case study in a lowland tropical rain forest in Peninsular Malaysia. In: Lambert JE, Hulm PE & Vander Wall SB (eds.) Seed Fate: Predation, Dispersal and Seedling Establishment. CABI Publishing, Oxfordshire, pp. 151–174.

Zahn W (1941) Die Riesen-, Streifen- und Spitznasenhörnchen der orientalischen Region. Zeitschrift für Säugetierkunde, 16: 1–182.