A tail of evolution: evaluating body length, weight and locomotion as potential drivers of tail length scaling in Australian marsupial mammals

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Although mammalian tail length relative to body length is considered indicative of locomotor mode, this association has been difficult to quantify. This could be because the counterweight function of the tail might associate it more with body weight than body length. Alternatively, relative tail length might not be evolutionarily flexible owing to its integration with the remaining skeleton, particularly the spine. Using comparative analyses of morphological means and ranges in Australian marsupials, including the first co-assessment with body weight, our study supports the second hypothesis, i.e. tail length ranges within species, and tail lengths among species are explained better by body length than by body weight. However, all three variables do not differ in phylogenetic signal or rates of evolution. Associations of tail lengths with locomotion are limited, but suggest that scaling slopes, rather than intercepts, are responsible for limited divergence between relative tail lengths at different locomotor modes. This complicates (palaeo-)ecological interpretations of tail length further. We conclude that relative tail length is not a strong predictor of locomotor mode, probably owing to strong integration of tail and body length. The many well-documented bony and soft-tissue adaptations of tails are likely to be better suited to interpretations of locomotor adaptations.

ADDITIONAL KEYWORDS: macroevolution – phylogenetic generalized least squares – vertebral column.

INTRODUCTION

Tail morphology has diversified throughout the evolution of mammals and is widely seen as an integral part of locomotion (Hickman, 1979). In particular, tail length relative to body length ('relative tail length') is thought to change the ability of the tail to act as a counterweight to support changes in torque during arboreal locomotion (Youlatos, 1999; Larson & Stern, 2006; Hayssen, 2008; Russo & Shapiro, 2011; Dalloz *et al.*, 2012; Russo, 2015), on uneven substrates (Schmidt & Fischer, 2011) or during bipedal hopping (Emerson, 1985). This association with locomotor function has made relative tail length a commonly-used predictor of locomotion in fossils and living mammals (reviewed by Russo, 2015). However, the role of locomotor mode in the evolution of relative tail length is not as quantifiable as might be

expected. For example, determinants of tail length in arboreal mammals are debated or not phylogenetically corrected (Hickman, 1979; Thorington & Heaney, 1981; Kohlsdorf *et al.*, 2001; Dudley *et al.*, 2007; Hayssen, 2008). In addition, the largest study of tail lengths to date, including 340 primates, found only leaping behaviour as a significant predictor among ten locomotor categories. Contrary to expectations (Hickman, 1979; Hayssen, 2008; Russo, 2015), that study also found no difference in relative tail length between arboreal and terrestrial species (Sehner *et al.*, 2018).

A possible explanation for the lack of locomotor signal in relative tail length might be its role as a counterweight. Thus, tail length might respond more to changes in weight than in body length (Grand, 1977; Russo, 2015), and body length might not be the primary predictor of tail length. Alternatively, tail length relative to body length might not be an efficient target for locomotor selection in the first place. Tails are part

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of the skeleton, specifically of the vertebral column, in which the serially homologous vertebral elements are highly integrated developmentally (Hautier *et al.*, 2010, 2011; Asher *et al.*, 2011; Jones *et al.*, 2018). This might prevent tail length from varying relative to body length or weight; for example, as shown in strong correlations of body and tail length in primates (Majoral *et al.*, 1997). Although variation in the number of vertebrae can change tail lengths, such as in the evolution of tail loss (Russo, 2015; Sehner *et al.*, 2018), the posterior vertebral column might more readily adapt its vertebral shape, muscular anatomy (Russo & Young, 2011; Russo, 2015; Young *et al.*, 2015; Jones *et al.*, 2018) or weight distribution (Grand, 1983, 1990). Also, individuals can experience high variation in weight throughout their lifetime (Mercer, 1998), and relative tail lengths can vary extensively within species (Thorington, 1970; Kaufman & Kaufman, 1992; Fooden & Albrecht, 1999). The capacity to accommodate large weight ranges relative to fixed tail lengths might therefore be intrinsic to mammals.

In this study, we provide the first quantitative investigation of how body weight and body length correspond to tail length, both in terms of within-species length ranges and on macroevolutionary time scales, using the marsupial mammals of Australia. These are a large, phylogenetically highly resolved, monophyletic radiation with a wide range of sizes (85 000 g–92 000 g) and diverse locomotor modes, including arboreal locomotion, hopping, terrestrial quadrupedal locomotion and scansoriality. This has made them a popular comparison in studies of primate locomotion (Weisbecker & Warton, 2006; Kirk *et al.*, 2008; Youlatos, 2008; Granatosky *et al.*, 2014; Youlatos *et al.*, 2018). We use a comprehensive dataset from the *Field companion to the mammals of Australia* (Van Dyck *et al.*, 2013; henceforth, '*Field companion*'), containing recently revised data collections for tail length, body length and body weight with their intraspecific ranges. Hypothesizing that relative tail is constrained by integration with body length, we make the following predictions:

1. Within species, tail length and body length should display similar range magnitudes. Also, species that have greater ranges of body length should have greater ranges of tail length;
2. Between species, tail length should be better explained by body length than by weight. We also expect body and tail length to scale in a similar manner with body weight, suggesting that they evolve as a unit. Different rates of evolution of body weight compared with body and tail length can also be an indication that weight and length evolve according to different patterns (although similar rates would not suggest that the opposite is true);

3. Tail length and locomotor mode should show little association, as found in primates (Sehner *et al.*, 2018). Most differences should occur where active use and biomechanical loading of the tail are expected to exert strong selection pressure to be of a certain length to function. This includes some kangaroo species, which use their tail as a load-bearing extra 'foot' during slow walking (Dawson *et al.*, 2015), and arboreal possums, for which tails are prehensile (Hickman, 1979; Dudley *et al.*, 2007).

MATERIAL AND METHODS

AVAILABILITY OF DATA AND CODE

All data and code used to assemble the data and replicate the analyses were conducted in R v.3.5.1 (R Core Team, 2018). All code and data are available from a public GitHub repository. The data and procedures outlined below refer to the addresses of files in this folder.

ASSEMBLING THE FULL DATASET FROM FIELD GUIDE ENTRIES

We collated a 'raw' dataset (Supporting Information, Supplementary File 1; 'Data/raw_data.csv' on GitHub) from the *Field companion*, including means and ranges for tail length, head and body length and body weight for each species. The measurements contained in the field guide were initially collected for the first edition of *The complete book of Australian mammals* (Strahan, 1983). They were updated for each of the subsequent two editions, by Strahan (1995) and Van Dyck & Strahan (2008). Each species account is authored by an expert on that species, using the expert's data. The submission protocol for the field guide stipulated that only adult measurements be entered, but determination of adult status was left to the expertise of each author. As for most field guides, this collection effort means that no database of original specimen measurements is available. However, for the *Field companion*, one of us (A.M.B.) revised the measurements for each species based on comprehensive investigations of museum specimens, resulting in a highly reliable, recently updated dataset. Note that the combination of head length into overall body length increases the risk of unrealistically low correlations between tail and body length, but this was deemed acceptable because the precaudal vertebral column generally dominates overall body length in mammals (see also use of a similar head/body length dataset by Sehner *et al.*, 2018).

Data on the mode of locomotion of species were collected from many independent sources (Menkhorst

& Knight, 2001; Van Dyck & Strahan, 2008; Woinarski *et al.*, 2014; Andrew, 2015; Baker & Dickman, 2018). Each species was assigned to one of four locomotor modes, representing common categories of tail use (Hickman, 1979; Hayssen, 2008; Sehner *et al.*, 2018): terrestrial quadrupedal, saltatorial, scansorial or arboreal. Note that nearly all arboreal species are also prehensile tailed, with additional separation of 'pentapedal' kangaroos using their tail as a 'fifth leg' based on Dawson *et al.* (2015) (see Table 1). The musky rat kangaroo, *Hypsiprymnodon moschatus*, can climb but is mostly terrestrial (Johnson & Strahan, 1982) and was scored as such.

Depending on the species, the *Field companion* gave data with different levels of resolution, but ~67% of species had average values either for the species or separately for males and females. A detailed breakdown of data resolution contributing to the raw dataset is shown in the Supporting Information (Table S1). To produce a single, maximally accurate value for each species, we computed species means and ranges using a succession of criteria. Wherever species averages and minimal/maximal values were given, these were used. If, instead, male and female averages and ranges were given, the species values were derived from male/female averages and the absolute minimal and maximal values of the species. In ~33% of species, no averages but only ranges were given. Out of these, the average of the range or, where present, the average of the sex ranges was used as the species data point. To assess whether this use of 'midpoints' was appropriate, we compared midpoint-derived values and means for those species where ranges and means (either overall or for the separate sexes) were available. Most of the body and tail length means were within 10% of the species mean (Supporting Information, Fig. S1), with an average midpoint value of 2.67 and 2.79% of the known mean, respectively. For weight, means were consistently overestimated by the midpoint, leading to more misestimates, which were on average still only 7.7% of the known mean.

Next, we created smaller datasets of male and female averages to assess whether the use of data from just one sex would change the significance levels of our phylogenetic generalized least squares (PGLS) analyses. All R code for this is repeatable on the original dataset in the GitHub repository under 'Analyses/01-Data Processing'. The derivative full dataset is also provided in the Supporting Information (Supplementary File 2) and the 'Data' folder of the GitHub repository.

Owing to the large range of sizes (85 000 g–92 000 g) in our dataset, we log$_{10}$-transformed all data. Six species of marsupials (the three wombats, two species of marsupial moles and the koala) were excluded from all analyses because their lack of a tail (or very reduced tail length in the case of moles) introduces extreme, potentially high-leverage outliers into the distributions of values (see GitHub file 'Data/02_preparation_for_analysis. rmd'). However, the distribution of our data was bimodal owing to a high number of very small-to-medium-sized species (Supporting Information, Fig. S2). This is not an issue if the residuals of the models computed are evenly distributed (Zuur *et al.*, 2010); therefore, we produced qq plots of residual normality using the *nlme* package, to ensure that there were no high-leverage outliers in the distribution of model residuals. Nearly all of these indicated a good residual fit, generally with a small number of slightly larger residuals on either end of the residual distribution. The only exception was our computation of correlation of ranges (see results section "Scaling of tail length with body length and weight" for details and caveats). The qq plots are not presented in this manuscript, but can be run as part of the code for each analysis in the 'Analysis/03-Analyses.rmd' file.

PHYLOGENY

The phylogeny we used was based on May-Collado *et al.* (2015). A small number of polytomies within the rock-wallabies (*Petrogale*) was broken up using the multi2di function of ape (Paradis & Schliep, 2018)

Table 1. The four locomotor categories, with descriptions and the terms from field guides used to classify each species

Category	Description
Terrestrial	Quadrupedal species that move primarily on the ground. This includes species classified as 'terrestrial' or 'mostly terrestrial'.
Arboreal	Species that move primarily via climbing through trees. This includes species classified as 'arboreal' or 'mostly arboreal'.
Scansorial	Species that spend considerable amounts of time moving both on the ground and climbing. This includes species classified as 'semi-arboreal' or 'arboreal and terrestrial'.
Saltatorial	Species that make extensive use of bipedal saltation ('hopping').
Pentapedal	Macropodine species that have either been shown to be pentapedal (using their tail as a 'fifth leg') based on Dawson *et al.* (2015) or their congenerics.

and their branch lengths replaced and given a small value (1% of mean overall branch length) to permit subsequent computations of phylogenetic signal and evolutionary rates. Although more recent phylogenies are available, this phylogeny was chosen because of its near completeness of taxon sampling and its congruence with widely held relationships between marsupial clades. However, 14 most recently described Australian marsupial species were excluded from the phylogenetic analysis, because no data on their phylogenetic positions were available, leaving 130 species in the analysis. Trees were pruned and matched to the datasets analysed using *ape* and *geiger* (Harmon *et al.*, 2008). This code is available in GitHub file 'Data/02_preparation_for_analysis.rmd'. The phylogeny, colour coded by locomotor mode, is shown in the Supporting Information (Fig. S3).

PHYLOGENETIC GENERALIZED LEAST SQUARES MODEL CONSTRUCTION

For all our tests of associations between tail length and other variables, we computed PGLS analyses using the R packages *nlme* (Pinheiro *et al.*, 2018) and *ape*, using the phylogeny described above. The PGLS algorithm also allowed us to compute two branch-length transformations [ultrametricized according to Grafen & Hamilton (1989) and Pagel (1992) and two evolutionary models, (Pagel's (1999) and Grafen's (1989) Brownian motion]. We determined the best combination of branch length and evolutionary model for each of our models by determining the relative likelihoods of each combination based on Akaike scores (*W*; Burnham & Anderson, 2002). This procedure identifies the differences between Akaike information criterion (AIC) values of each model and uses this information to allocate a proportional likelihood for each of the models, with all likelihoods adding up to one (see 'utilities' file for the implementation). Determination of the best model was implemented in the 'find.best.model' function, which can be sourced in our utilities file on GitHub ('Analyses/Utilities'). We computed the ANOVA table for the best combination. For models with more than one predictor variable, we used a type III ANOVA from the *car* package (Fox & Weisberg, 2011), which adjusts for the effect of all other predictors before testing each separate predictor variable. In models with several predictors, we also first tested whether there was a significant interaction term between predictor variables. If the ANOVA table revealed no significant interaction, we re-ran the model with the interaction removed.

SEX DIFFERENCES

It is possible that systematic differences in the evolution of male and female tails might result in different scaling of tail length with body length or mass between sexes (Sehner *et al.*, 2018). We used a non-phylogenetic type III ANOVA to assess whether the slopes or intercepts of tail length with body weight/length within our locomotor categories differed between male-only or female-only datasets. Note that a phylogenetically informed analysis of multiple data points per species is not straightforward (Garamszegi, 2014; Symonds & Blomberg, 2014) and was therefore not conducted.

RANGE VARIATION

To assess within-species variability of weight, tail and body length, we divided the maximal value of each trait by the minimal value, meaning that a low range is closer to one and a higher range is represented by multiples of the minimal range. We plotted the distributions of ranges for each variable as boxplots and ran a pairwise Wilcoxon rank sum test from the *stats* package (R Core Team, 2018) to assess whether there were significant differences in mean range between body length and tail length. Given that we noted particularly large ranges in the order Peramelemorpha (bandicoots and bilbies), where maximal weight can be more than six times greater than minimal weight, we also plotted and analysed the dataset without representatives of this clade. We also conducted a phylogenetic ANOVA using the *Phytools* package (Revell, 2012) to ask whether the ranges of arboreal and pentapedal species were significantly smaller than those of other species, which would point to a functional constraint on tail size in these species. Lastly, we used PGLS to ask whether species with greater ranges of tail length also had greater ranges in weight, testing the hypothesis that integration between tail length and weight should produce a strong correlation between the two.

EVOLUTIONARY RATES AND PHYLOGENETIC SIGNAL

Comparisons of body/tail length and weight evolution were conducted by first using the fit.continuous function of the *Phylo* (Revell, 2012) package to establish that each of the scaled traits were most likely to evolve under Brownian motion, which is an assumption of the comparison of evolutionary rates

Table 2. *W*-Scores according to Burnham & Anderson (2002), determining which model of evolution fits the separate data best, showing that a Brownian motion model fits the data best in all three BM, Brownian motion; OU, Ornstein-Uhlenbeck; EB, Early burst

	BM	OU	EB
Log_{10}(tail length)	0.57	0.20	0.22
Log_{10}(body length)	0.47	0.16	0.36
Log_{10}(body weight)	0.53	0.19	0.27

(Table 2). We then used the *phylosig* function in *Phylo* to assess the phylogenetic signal within each trait, using Blomberg′s k (Blomberg, 2003). Subsequently, the rates of evolution between *z* scores of all three traits were compared, using the compare.multi.evol. rates function in *geomorph* (Adams, 2014). The *z* score transformation (which scales each trait to have a mean of zero and a standard deviation of one) was necessary to enable a meaningful comparison between the differently scaled body and tail lengths vs. body weights.

SCALING OF TAIL LENGTH WITH BODY LENGTH AND WEIGHT

To assess whether tail and body length scaled in a similar manner with body weight, we compared the scaling coefficients of each against weight in a PGLS model. To assess whether tail length was better explained by body length or weight, we compared AIC values for models with tail length as a dependent variable and body length or weight as predictor variables. In addition, a type III ANOVA was conducted of a PGLS model of tail length as a dependent variable and both body length and weight as predictor variables, to assess significance levels and coefficients after adjusting for each.

LOCOMOTOR CORRELATES OF TAIL LENGTH RELATIVE TO BODY LENGTH AND WEIGHT

To assess whether locomotor mode was a significant predictor of tail length, we first computed a PGLS model with tail length as the dependent variable and body length or weight as predictor variables according to the PGLS methods outlined above. Unfortunately, post hoc tests of significant differences in slope or mean in a phylogenetic context are currently not available; therefore, we used non-phylogenetic post hoc tests to provide a tentative further investigation. These come with a caveat of not being phylogenetically corrected and thus might exaggerate significances where a locomotor mode is attributable to a single transformation at the base of a clade (Felsenstein, 1985). They are considered here with these caveats in mind. For assessments of differences in slope, we used the pairwise function of the RRPP package (Collyer & Adams, 2018).

Locomotor mode is strongly associated with clade affiliations, with group aggregation according to locomotor mode particularly at order and/or family level in marsupials (Weisbecker & Warton, 2006; see also Supporting Information, Fig. S3), which represents a challenge for the correct estimation of significance levels (Adams & Collyer, 2018). Hence, even with the PGLS analysis there might be a separate influence of

phylogenetic affinity at this particular taxonomic level. We therefore added a PGLS analysis asking whether affinity to a major marsupial clade (order or family) has a significant association with tail length scaling.

Lastly, for a combined visual evaluation of within-species variability and between-species scaling, we produced a scatterplot of mean tail lengths against mean body lengths or weights, with minimal and maximal ranges of each species superimposed as ellipses.

RESULTS

SEX DIFFERENCES

There was no difference in scaling slope or intercept of tail length against either body length or weight when the smaller all-male or all-female datasets were analysed separately or when either was compared with the dataset of average values (Table 3; for scatterplots and regression lines, see also Supporting Information, Fig. S4). We therefore continued all further analyses with averages and ranges from both sexes.

RANGE VARIATION

Tail and body length ranges did not have significantly different means (both had maximum 1.44 times the minimum; Fig. 1). On average, the maximal weight within a species was 2.64 times greater than the minimal weight. Similar results were obtained when excluding the highly variable peramelemorphs (bandicoots and bilbies; see Supporting Information, Fig. S5). Phylogenetic ANOVAs showed that arboreal and pentapedal species did not differ significantly from other species in their range of tail lengths ($P = 0.92$), body lengths ($P = 0.833$) and body weights ($P = 0.9$). The PGLS modelling of tail length ranges against body length and weight ranges showed that species with greater tail length ranges also displayed greater body length ranges (slope coefficient 0.68, $P = 0.000$) and, with a shallower scaling slope, weight ranges (slope coefficient 0.13, $P = 0.000$).

EVOLUTIONARY RATES AND PHYLOGENETIC SIGNAL

All three variables displayed a high phylogenetic signal, with *k* values much greater than one, indicating stronger similarity of all three variables between related species than expected under Brownian motion. Tail *z* scores also had slightly faster rates of evolution compared with body length and weight, but these differences were not significant (Table 4).

Table 3. A summary of the results derived from the main model of tail length against various predictor variables

Modelling	Pred. 1	Pred.2	Interact. term	Slope	F/t (Pred. 1)	P (Pred. 1)	F/t (Pred. 2)	P (Pred. 2)
LM	Body length	Sex (lm)	n.s.		2136	**0.000**	0.044	0.95
LM	Weight	Sex (lm)	n.s.		2274	**0.000**	0.04	0.96
PGLS	Body length			0.8	13.7	**0.000**		
PGLS	Weight			0.27	13.04	**0.000**		
PGLS	Body length	Body weight	n.s.		11.6	**0.001**	3.76	**0.05**
PGLS	Body length	Loco. Mode	0.01					
PGLS	Weight	Loco. Mode	0.02					
PGLS	Body length	Loco. Mode (no peramelemorphs/ *Macropus*	0.01					
PGLS	Body length	Clade	n.s.		185.6	**0.000**	0.59	0.67
PGLS	Body weight	Clade	n.s.		0167.7	**0.000**	0.54	0.71

Terminology: 'Modelling' indicates whether conventional linear models (LM) or phylogenetic generalized least squares (PGLS) models were used (see Material and Methods section for justification); 'Pred. 1/Pred. 2', predictor variables used; Interact. term, *P*-values for significant interactions or 'n.s.' for no significant interaction term; 'Slope' is the slope for the two models using body length and weight as predictors; *F/t*, *F* or *t* values for each predictor in models without significant interaction terms; and *P*, *P*-values for the probability that no association exists. Significant (< 0.05) *P*-values are in bold. Loco. Mode, locomotor mode. Note that the optimal model for all phylogenetic generalized least squares (PGLS) analyses was based on untransformed branch lengths and Brownian motion correlation structure, with one exception (see main text).
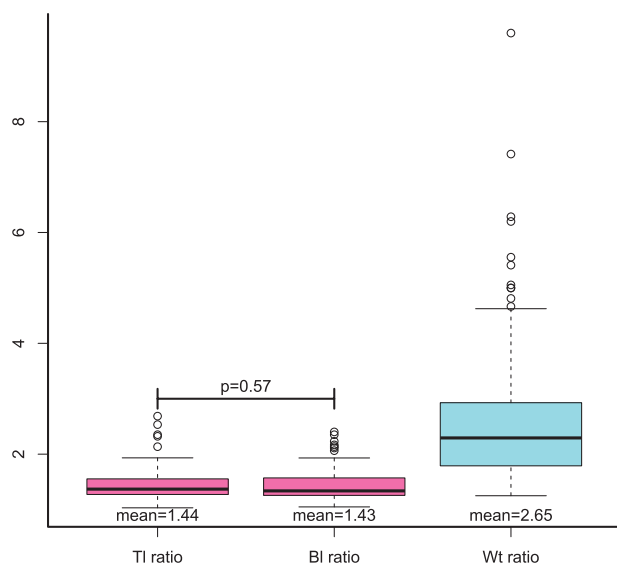

Figure 1. Boxplots of ranges (maximum/minimum) within species for tail length ('Tl ratio'), body length ('Bl ratio') and weight ('Wt ratio'). The horizontal line represents the results of pairwise Wilcoxon rank sum tests of differences in the mean between tail and body length range ratios.

SCALING OF TAIL LENGTH WITH BODY LENGTH AND WEIGHT

Using *W* score comparisons of the AIC values revealed that body length range was a far more likely predictor of tail length range than body weight range (*W* scores 0.999 vs. 0.000, respectively). Note that

the distributions of residuals for the range models suggested a poor model fit, thus adding a caveat to these results. However, the strong difference in *W* scores suggested that the result reflected a real pattern. Comparing PGLS models of tail length with body length and weight as predictors revealed highly significant associations with both variables (Table 3). In both cases, scaling of tail length against body length and weight occurred with negative allometry, with a substantially lower slope coefficient for weight (0.27) than for length (0.8). Akaike information criterion comparison of the two models revealed that the model using body length explained tail length far better (*W* score of 0.99) than the model that used weight (*W* score of 0.008). A PGLS model with body weight and length as covariates showed no significant interaction between the two. Dropping the interaction showed that body length retained a significant association with tail length when corrected for weight, but the association with weight dropped slightly below the significance threshold after correcting for body length (Table 3).

LOCOMOTOR CORRELATES OF TAIL LENGTH RELATIVE TO BODY LENGTH AND WEIGHT

Figure 2 depicts scatterplots of the association between tail length vs. body length and tail length vs. body weight, with notations of locomotor mode and clade affinity and using the PGLS coefficients as slopes. In the PGLS models of tail length with body length/ weight and locomotor mode as covariates, there were significant interaction terms between locomotion and

Table 4. Comparison of evolutionary rates of tail length, body length and weight on a Grafen-transformed phylogeny

	Phylog. signal (K)	Log_{10}(tail length)	Log_{10}(body length)	Log_{10}(weight)
Log_{10}(tail length)	1.31	2.44	0.35	0.086
Log_{10}(body length)	1.51	1.15	2.08	0.405
Log_{10}(weight)	1.75	1.35	1.17	1.8

'Phylog. signal' is Blomberg's K statistic of phylogenetic signal. The rates are shown on the diagonal. Rate ratios are shown in the lower triangle, and P-values are in the upper triangle.

body length or weight (Table 3). Visual examination of the plots in Figure 2 leads us to suspect that the significance of interaction terms might be driven by the peramelemorphs (which all have substantially shorter tails than other marsupials of their size) and the kangaroo genus *Macropus* (which seemed to scale in a different manner to all other species). However, removal of these two groups did not lead to non-significant interaction terms (Table 3). To assess whether the strong association of locomotor mode with major marsupial clades (orders/families) was responsible for our associations between locomotor mode and tail scaling, we add a PGLS model of tail length vs. body length/weight with major clade as covariates. This showed no significant interactions/means according to order/family (Table 3), increasing confidence in our results of locomotor scaling. However, the results were still at risk of exaggerated significances in cases where a locomotor mode changed at the base of a clade (Adams & Collyer, 2018); therefore, we considered them cautiously here. Using a non-phylogenetically corrected post hoc test to assess interactions between locomotor modes and body length/weight suggested several scaling slope differences (Table 5). Note the explicit caveat that the interaction test results might be phylogenetically confounded and thus might not be significant in a phylogenetic context. They should therefore be interpreted only while bearing in mind the strong phylogenetic component visible in Figure 2.

To gain further resolution into possible intercept differences between locomotor modes with no significant non-phylogenetic interaction terms, we ran separate PGLS analyses of datasets including locomotor modes that have no significant interaction term in the overall models. These suggested a low-significance difference in means between terrestrial and pentapedal species as the only possible difference (Table 6).

Overlaying minimal and maximal ranges of individual species over each data point suggested extensive overlaps in the relationship between tail length and body length (Fig. 3).

DISCUSSION

Our use of a detailed field guide allowed the first quantitative assessment of tail length relative to body length and weight, in addition to within-species range variation, in a mammalian clade with nearly three orders of magnitude of variation in body weight and containing diverse locomotor modes. This confirmed our expectation that tail length is more strongly determined by body length than body weight. Particularly within species, tail length and body length have near-identical range magnitudes that are much narrower than the weight ranges. Tail and body length range magnitudes are also significantly associated with each other. In contrast, weight ranges are both more variable than either tail or body length ranges and associated with body or tail length range at lower levels of significance. This confirms our expectation that the tails of individuals can cater for a variety of weights within species, suggesting that the use of the tail in the balancing of weight during locomotion might not be a primary determinant of tail length. This might also be the reason why this and a recent study on Primates (Sehner *et al.*, 2018) find only low or moderate support for differences in relative tail length according to locomotor mode. Instead, several commonly occurring adaptations might accommodate such changes in weight distribution, including by adjustments of the muscular system (Russo, 2015), gait adjustments (Siegel, 1970; Igarashi & Levy, 1981; Young *et al.*, 2015) or changes in the distribution of body fat (Tribe & Peel, 1963; Morton, 1978; Pond, 1978; Hickman, 1979).

In a macroevolutionary context, AIC comparisons of our PGLS analyses show that body length explains tail lengths far better than body weight; this is also reflected in the lower levels of significance in the association of weight relative to tail length after correcting for body length. Thus, the scaling between tail and body length is likely to be determined by close association between body length and tail length, rather than body weight. The PGLS analysis shows that body length and tail length scale with body weight at slope exponents of 0.27 and 0.32, suggesting that both evolve in a pattern close to geometric similarity scaling with body weight, which exists for mammalian body length (Silva, 1998) and many (but not all) mammalian limbs (Campione & Evans, 2012). These
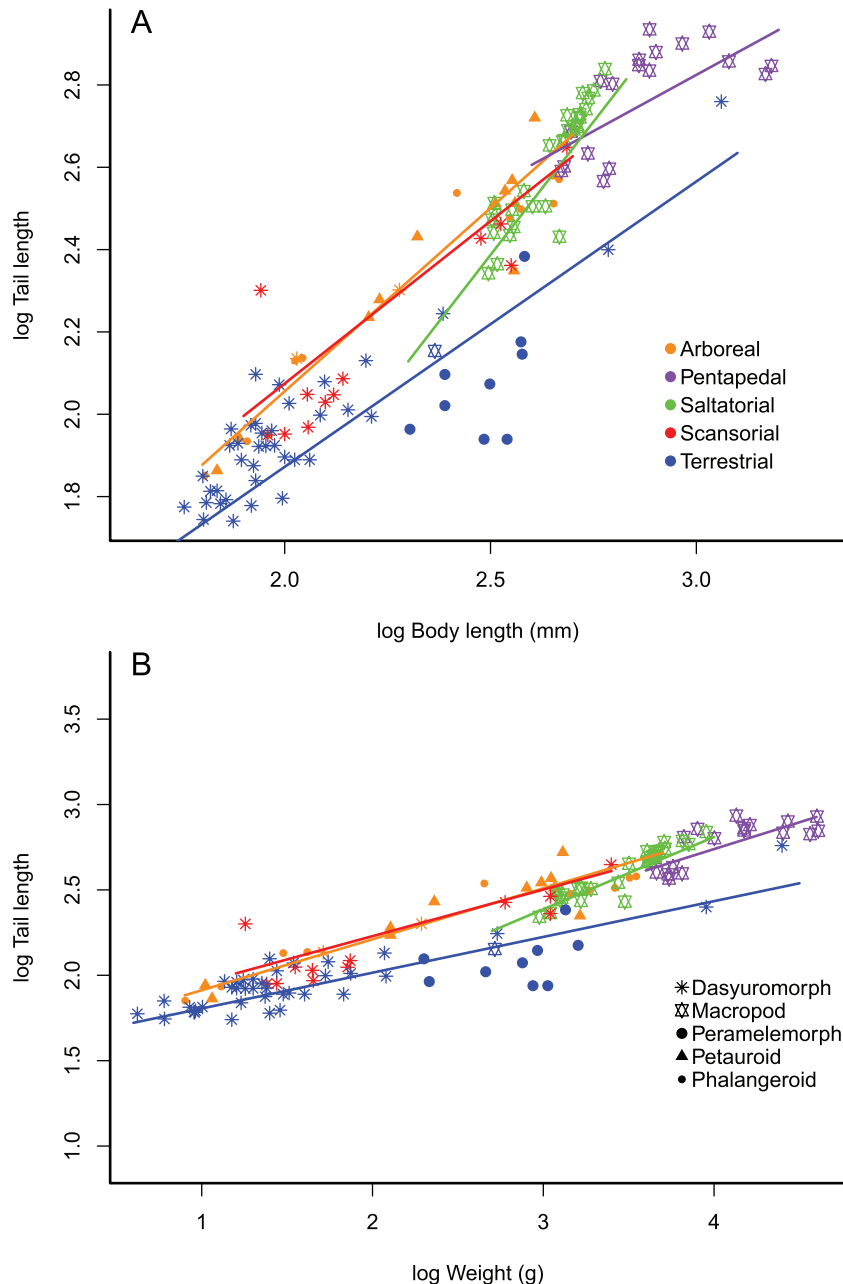
Figure 2. Scatterplots of the association between tail length vs. body length (A) and between tail length vs. body weight (B), with colour notations of locomotor mode and major clade affinity. The slopes are based on phylogenetic generalized least squares coefficients of tail length scaling for each locomotor mode.

results support our expectation that body and tail length represent a developmentally integrated (Jones *et al.*, 2018) vertebral column system that acts as a scaffold for, but does not readily adapt to, changes in weight. An intriguing possibility for further study is that the effects of integration might extend more generally across the skeleton. For example, Sehner *et al.* (2018) suggested that the association between primate tail length and leaping locomotion might be related to pleiotropic effects of higher intermembral

indices, which are also associated with leaping. This also raises the possibility that the strong association between the precaudal vertebral column and the tail arise from the fact that the whole skeleton is a better indicator of body size in comparative study than body weight, which might be more variable overall. Further studies including limb measurements will be required to decide this.

Counter to previous expectations, associations of locomotor mode with relative tail length are not clear,

Table 5. Non-phylogenetically corrected post hoc *P*-values for interaction terms for tail length vs. body length/weight and locomotion

	Pentapedal	Arboreal	Saltatorial	Scansorial	Terrestrial	Allometric slope using body length
Pentapedal		0.081	0.001	0.243	0.929	0.54
Arboreal	0.382		0.008	0.622	0.001	0.85
Saltatorial	0.034	0.023		0.002	0.001	*1.44*
Scansorial	0.481	0.778	0.033		0.044	0.78
Terrestrial	0.672	0.002	0.001	0.043		0.53
Allometric slope using body weight	0.21	0.28	0.43	0.27	0.18	

Upper triangle is for scaling of tail length with body length, lower triangle for scaling of tail length with body weight. Italic highlights the slope indicating positive allometry.

but are dominated by significant differences of scaling slope, rather than mean, between several locomotor modes. In particular, the tail and body length scaled in a significantly different manner in terrestrial and saltatory species compared with others. This result challenges the general applicability of the suggestion that differences in mean tail length are good indicators of locomotor mode, particularly when distinguishing arboreal from terrestrial species (Thorington & Heaney, 1981; Hayssen, 2008; Russo, 2015; Sehner *et al.*, 2018). Instead, the size of species seems to play an important part in this distinction; the slopes and distribution of species on the scatterplots suggest that larger arboreal species do have longer tails than others, but that there is broader overlap at arboreal smaller sizes.

Although it is difficult to interpret the scaling differences between locomotor modes, it is notable that species with tails that have a more exclusive counterbalance function, such as arboreal and saltatory species, have the highest scaling slopes in our sample, although the differences in slopes mean that this does not result in clear overall differences in tail length. This effect is particularly striking in comparisons between pentapedal ('tail-walking') vs. saltatory kangaroos. In pentapedal species, tail length increases by only half a unit for every unit of body length increase, whereas in saltatory species, tail length increases 1.5 times with each unit of body length extension. These slopes are probably exaggerated owing to the relatedness of saltatory and pentapedal species, but strongly suggest a switch from positive to negative allometry in the two locomotor modes. Expectations that the counterbalancing function of the tail impacts on relative tail length evolution (Youlatos, 1999; Larson & Stern, 2006; Hayssen, 2008; Russo & Shapiro, 2011; Dalloz *et al.*, 2012; Russo, 2015) might therefore be justified, but not in the context of tail length means as previously suggested. However, this effect is not strong and needs to be verified in a broader mammalian sample.

Our results showing subtle scaling differences according to locomotor mode are consistent with findings that the posterior vertebral column has a more variable number of vertebrae in mammals (Asher *et al.*, 2011). It also matches recent results showing that the more posterior lumbar spine vertebrae display more shape disparity, higher evolutionary rates and greater ability to adapt their shape to locomotion than the more anterior thoracic vertebrae (Jones *et al.*, 2018). However, this variability does not seem to manifest strongly in the evolution of tail length, because it neither shows significantly faster evolutionary rates nor does it differ much in phylogenetic signal. Thus, despite a moderate influence of locomotion on tail length, our results overall are more consistent with our expectation that the main targets of locomotor selection on the spine might be other anatomical features.

Mapping individual ranges of minimal and maximal tail/body length and body weight suggests substantial overlap in tail proportions between species adopting different locomotor modes. Data on the scaling of all variables among individuals were not available, but it is likely that they follow a particular scaling slope within each species. For example, on average, the maximal body weight of a species is 2.6 times the minimal, and the range of body and tail length is ~1.44. This value is close to what would be expected under geometric similarity scaling ($2.6^{0.3} = 1.34$). However, even if all species follow a tight scaling slope, the overlaps of range appear sufficiently great as to obscure any macroevolutionary effects of locomotor mode on relative tail length. This adds an additional note of caution to interpretations of relative tail length in contexts of locomotion, despite the intriguing scaling patterns we find in the species averages.

CONCLUSIONS

Our study supports our expectation that high integration of the tail with overall body length (and,
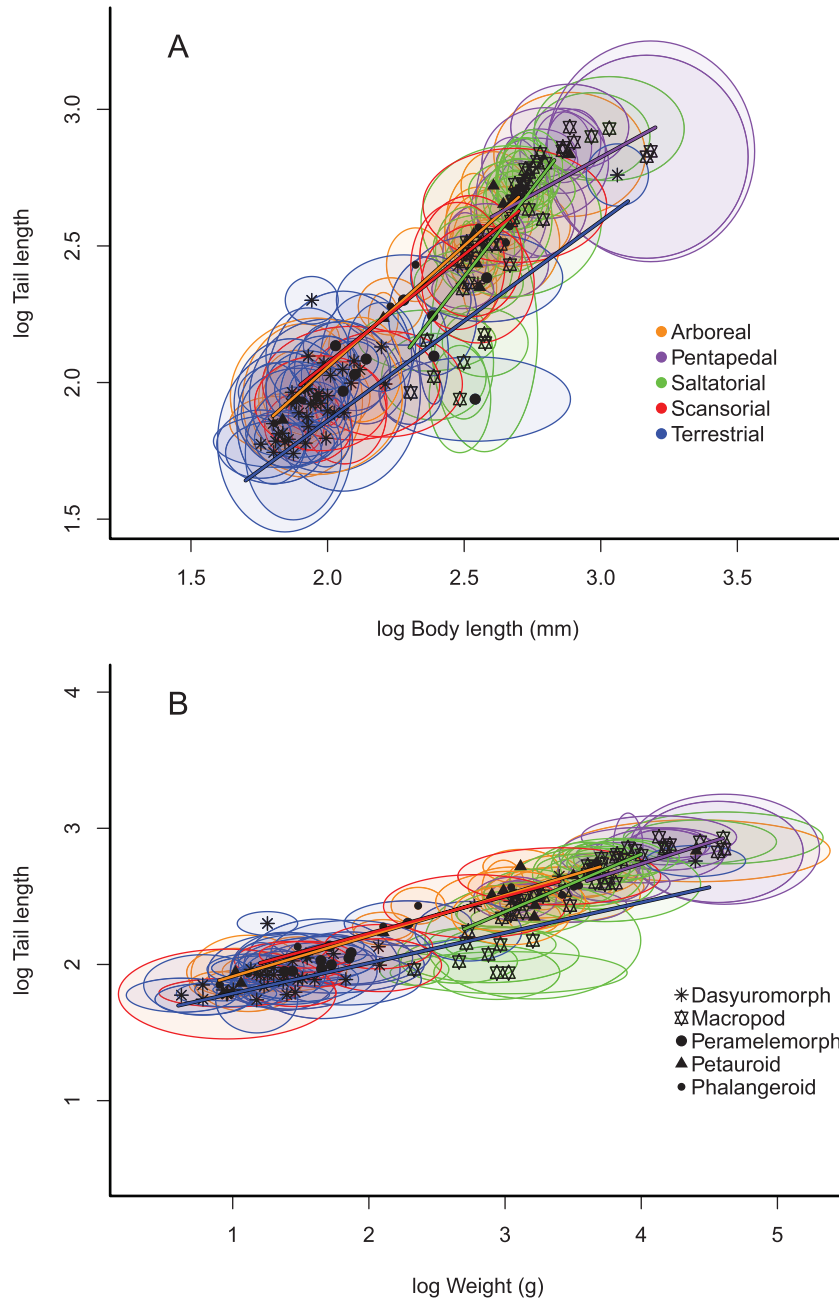
Figure 3. Scatterplots of the association between tail length vs. body length (A) and between tail length vs. body weight (B), with minimal/maximal ranges for each species superimposed (the height and width of ellipses represent minimal/maximal log *x* and log *y* values, respectively). The lines are phylogenetic generalized least squares lines, as in Figure 2.

possibly, the skeleton overall) might be an important factor in the evolution of relative tail length, with the additional insight that extensive within-species ranges of tail and body length suggest high levels of flexibility in how a tail is used by individuals. We find only limited and ambiguous evidence for scaling slope differences of tail length according to locomotor mode. This reinforces our initial suspicion that the evolution of the balancing function of the tail might be most heavily influenced by anatomical adaptations not related to tail length, which are indeed common among mammals. For example, prehensile-tailed carnivorans and primates vary in the proportions of their tail regions (Youlatos, 2003; Schmitt *et al.*, 2005), prehensile-tailed and pentapedal marsupials have heavier tails (Grand, 1977, 1983, 1990), and reduction of tail length tends to co-occur with

Table 6. Results from phylogenetic generalized least squares (PGLS) analyses of separate datasets assessing whether tail length scales with body length or weight, with different intercepts

Locomotor mode comparison	Length/weight F	Length/weight P	Locomotor mode F	Locomotor mode P
$\text{Log}_{10}(\text{tail length}) \sim \text{log}_{10}(\text{body length}) + \text{locomotor mode}$				
Arboreal–pentapedal–scansorial	136.3	**0.000**	0.003	0.96
$\text{Log}_{10}(\text{tail length}) \sim \text{log}_{10}(\text{body weight}) + \text{locomotor mode}$				
Arboreal–pentapedal–scansorial	158.57	**0.000**	0.20	0.66
Pentapedal–terrestrial	94.5	**0.000**	5.29	**0.025**

The locomotor modes investigated here are only those that were shown not to have significant interactions as presented in Table 5.

anatomical changes in the tail (Russo, 2015) and sacrum (Russo & Shapiro, 2011) in a variety of mammals. In addition, experimental evidence that mammals adjust their gait when their tails are experimentally shortened (Siegel, 1970; Igarashi & Levy, 1981; Young *et al.*, 2015) suggests that behavioural adjustments might allow optimal tail use for a range of lengths.

Our result needs to be confirmed in a larger sample of mammals and, possibly, with more highly resolved within-species variation, because we only had ranges available. However, we expect that our results on marsupials might be conservative compared with placentals. This is because the posterior skeleton of marsupials develops late during ontogeny and has some developmental independence from the anterior skeleton (Weisbecker *et al.*, 2008; Goswami *et al.*, 2009), which has been suggested to allow posterior parts of the marsupial body to display greater morphological disparity (Kelly & Sears, 2011). The evolution of marsupial relative tail length might therefore also be less constrained relative to the front of the body, compared with placental mammals. Another caveat of this study and others is the persistent heavily phylogenetically confounded distribution of locomotor modes in mammals, increasing the risk of a strong effect of phylogenetic correction. However, our results offer some inroads into explaining why relative tail length by itself has not been successful as a predictor of locomotor mode in mammals. We highlight the need to co-interpret tail length data in the context of scaling patterns and together with anatomical proxies of locomotion in cases where inferences on the locomotion of extinct mammals are made (see also Russo & Shapiro, 2011; Russo, 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Frequency histogram of the distribution of absolute deviation of midpoint estimates from the known mean, expressed as a percentage of the known mean.
Figure S2. Frequency histogram of the distribution of all three variables, showing bimodal distributions for all three.
Figure S3. Phylogeny used in this study, colour coded by locomotor mode allocated to each species.
Figure S4. Scatterplots of male, female and combined data points. Note that there are more combined data points, because some species did not have separate data for males and females.
Figure S5. Range ratio boxplots, as in Figure 1, with peramelemorphs removed.
Table S1. Percentage of values found in the raw dataset. The last six rows reflect instances where ranges, but not means, were present either overall or for the sexes. These are computed based on the presence of body length means and ranges.

SHARED DATA

All code and data are available from public GitHub repository https://github.com/VWeisbecker/Tails.