Big cat, small cat: reconstructing body size evolution in living and extinct Felidae

A. R. CUFF*†, M. RANDAU*, J. HEAD‡, J. R. HUTCHINSON†, S. E. PIERCE§
& A. GOSWAMI*¶

*Department of Genetics, Evolution & Environment, University College London, London, UK
†Structure & Motion Lab, The Royal Veterinary College, North Mymms, Hatfield, Herts, UK
‡Department of Earth and Atmospheric Sciences and Nebraska State Museum of Natural History, University of Nebraska-Lincoln, Lincoln, NE, USA
§Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA
¶Department of Earth Sciences, University College London, London, UK

Abstract

The evolution of body mass is a fundamental topic in evolutionary biology, because it is closely linked to manifold life history and ecological traits and is readily estimable for many extinct taxa. In this study, we examine patterns of body mass evolution in Felidae (Placentalia, Carnivora) to assess the effects of phylogeny, mode of evolution, and the relationship between body mass and prey choice in this charismatic mammalian clade. Our data set includes 39 extant and 26 extinct taxa, with published body mass data supplemented by estimates based on condylobasal length. These data were run through 'SURFACE' and 'bayou' to test for patterns of body mass evolution and convergence between taxa. Body masses of felids are significantly different among prey choice groupings (small, mixed and large). We find that body mass evolution in cats is strongly influenced by phylogeny, but different patterns emerged depending on inclusion of extinct taxa and assumptions about branch lengths. A single Ornstein–Uhlenbeck optimum best explains the distribution of body masses when first-occurrence data were used for the fossil taxa. However, when mean occurrence dates or last known occurrence dates were used, two selective optima for felid body mass were recovered in most analyses: a small optimum around 5 kg and a large one around 100 kg. Across living and extinct cats, we infer repeated evolutionary convergences towards both of these optima, but, likely due to biased extinction of large taxa, our results shift to supporting a Brownian motion model when only extant taxa are included in analyses.

Introduction

Body mass evolution in mammals has been a focus of study since Cope first suggested that there was a directed trend towards larger body mass throughout the Cenozoic Era (Cope, 1887). More recent studies have come to question whether Cope's Rule applies broadly across large clades, with suggestions that the apparent increases in body mass could be associated with an increase in variance, with no increase in smaller body sizes (i.e. a passive trend, Cope's rule *sensu lato*), and that only size increase in both lower and upper bounds, an active trend, should be recognized as Cope's rule *sensu stricto* (Stanley, 1973; McKinney, 1986; Gould, 1988; McShea, 1994; Arnold *et al.*, 1995; Novack-Gottshall & Lanier, 2008). Alongside these epistemological refinements, which improve the ability to derive process from pattern of body size evolution, there have been vast improvements in analytical tools which allow for rigorous reconstructions of within-lineage trends (e.g. Ingram & Mahler, 2013; Uyeda & Harmon, 2014).

With regard to body size evolution in mammals, it has been suggested that there is a natural optimum for mammals (Stanley, 1973; McKinney, 1986). Alroy (1998), however, found that there is not one optimum,

Correspondence: Andrew R. Cuff, GEE, University College London, Darwin Building, Gower Street, London WC1E 6BT, UK.
Tel.: +44 2076797117; fax: +44 2076797193; e-mail: andrew.cuff@ucl.ac.uk

but in fact two stable optima for mammals (at large and small body sizes), as well as an unstable one at medium sizes. This pattern does not hold for all mammal taxa, with canids trending towards larger sizes through much of their deep evolutionary history (Van Valkenburgh *et al.*, 2004), but more recently moving into the medium-sized, supposedly unstable optimum (Finarelli, 2007). Here, we present an analysis of body mass evolution in Felidae (cats), a particularly important group considering studies indicate cats are keystone and/or apex predators in many diverse ecosystems (Sunquist & Sunquist, 2002; Macdonald & Loveridge, 2010) and are severely under threat by poaching and habitat destruction (Macdonald & Loveridge, 2010). As such, understanding body size evolution (and relationship to prey size) in cats has immediate significance.

Felids are a family-level clade of Carnivora, comprising all of the extant cats, as well as many extinct taxa. The exact timing of the origin of felids is debated, but it is widely accepted that *Proailurus* is the most basal taxon, appearing in the latter part of the Oligocene (33.9–23 million years ago) (Peigné, 1999; Rothwell, 2003; Piras *et al.*, 2013). Within Felidae, there are at least two subfamilies, Felinae (crown group Felidae: all extant cats and their closest relatives) and the extinct Machairodontinae (sabre-toothed cats, Martin *et al.*, 2000), although several extinct taxa are not clearly affiliated with either subfamily (McKenna & Bell, 2000; Piras *et al.*, 2013). Within the extant felids, there is a large range of body masses, from a minimum mass of around 1 kg in the rusty footed cat to a maximum mass of around 300 kg in the largest tiger subspecies (Sunquist & Sunquist, 2002). This considerable body mass range is expanded by inclusion of extinct felids, with some attaining masses up to an estimated 410 kg (Peigné *et al.*, 2005). This body mass range has inspired discussions focusing on posture, prey capture and locomotory ability (Day & Jayne, 2007; Doube *et al.*, 2009; Meachen-Samuels & Van Valkenburgh, 2009a,b, 2010; Meachen *et al.*, 2014). Understanding how body mass evolved in this clade, and its relationship to phylogenetic history, is an important first step in addressing these biomechanical and ecological questions. To that end, we attempt to ascertain whether body mass evolution in living and extinct felids fits a model of Brownian motion or whether it is better explained by a more complex pattern through geological time.

Materials and methods

Body mass data

Body mass data were derived from primary literature where possible, but where no data existed for five of the taxa, estimates were made based on skull measurements (Table S1) using the formula:

$$\log_{10} \text{body mass} = \frac{\log_{10} \text{condylobasal length} - 1.723}{0.345}$$

which was derived from extant *Panthera* species (Mazák *et al.*, 2011) with an $r^2 = 0.968$. Taxa for which adequate cranial measurements or published body mass estimates were not available were excluded from further analysis. The final data set included 65 taxa, 39 of which are extant and 26 are fossils, ranging from 0.01 to 20.43 million years ago (Table S1). These taxa span most of the extant 41 species (Wozencraft, 2005), several of their closely related extinct relatives, the majority of tribes within the Machairodontinae, and *Proailurus lemanensis*, the most basal felid. Our sample represents the entire spectrum of body masses for felids, from the smallest felid (the extant rusty footed cat: 1.35 kg, Sunquist & Sunquist, 2002) to estimated largest taxon (the extinct *Amphimachairodus kabir*: 410 kg, Peigné *et al.*, 2005). All data were natural-log-transformed (ln) prior to analysis.

Phylogenetic tree

We applied phylogenetic comparative methods to body mass evolution in Felidae, using a recently published phylogenetic tree for living and extinct Felidae (Piras *et al.*, 2013) in all of the following analyses. This published phylogeny is a composite drawn from various literary sources. The topology for the extant felids and their closest relatives (Felinae: Piras *et al.*, 2013) was based primarily on genetic data from Johnson *et al.* (2006) and was modified to include new fossil felids described since 2006, several of which had the effect of increasing the divergence estimates of basal nodes (Piras *et al.*, 2013). Although this tree excludes some important fossil taxa (particularly some extinct *Panthera* spp.: Mazák *et al.*, 2011; Tseng *et al.*, 2014), it provides the most inclusive dated phylogeny available at present for living and fossil Felidae. The first, mean and last known occurrences of all taxa were used in separate analyses to represent the potential temporal range from which the fossil material may come and thereby bracket the possible effects of uncertainty in dating of fossil occurrences and knock-on effects for dating the phylogenetic tree. In addition, a dated phylogeny sampling only extant taxa was used to estimate the effects of the extinct taxa on our results. For all phylogenies, it was assumed that for all extant species, the masses are from modern material and so their branch lengths did not change.

Analyses

All analyses were conducted in R 3.1.0 (R Core Team 2014). We first assessed phylogenetic signal in the felid body mass data set using the phylosignal function in the 'picante' package (Kembel *et al.*, 2010). This func-

tion measures phylogenetic signal with K: a value reflecting the difference between the observed tip data and the expected values under a Brownian motion model for any given phylogeny (Blomberg *et al.*, 2003). A value for K close to 1.0 suggests a Brownian motion pattern, whereas values <1.0 indicate less resemblance to relatives than would be expected under Brownian motion; values >1.0 indicate more resemblance to relatives than would be expected (Kembel, 2010). Whereas the K statistic assesses the fit of a Brownian motion model, the p-value reflects the phylogenetic signal in the data set, with a significant result indicating that there is a significant phylogenetic signal in the data.

We then assessed the pattern of body mass evolution in felids using a series of standard models of trait evolution [Brownian motion, white/stasis, (directional) trend, Ornstein–Uhlenbeck (OU) and early burst] in the 'geiger' package (Harmon *et al.*, 2008). The models were compared using small-sample-corrected Akaike's information criterion (AICc), which compares the fit of each model relative to the other models, with a correction for finite sample sizes and a penalty for increases in model complexity.

We additionally conducted two exploratory analyses of body mass evolution using the 'SURFACE' package (Ingram & Mahler, 2013) and the 'bayou' package (Uyeda & Harmon, 2014). The 'SURFACE' approach fits OU models with increasing numbers of adaptive peaks to the data set, using stepwise AICc for model selection (Ingram & Mahler, 2013). This method also allows for the identification of convergence in trait evolution across a clade by identifying instances where different subclades approach the same selective optimum. However, this assumes the alpha (relative strength of attraction/pull towards the optima) and sigma-squared (the Brownian rate) values throughout the clade are treated as constant. If multiple-optima models were better supported than Brownian motion in 'SURFACE', the multiple-optima tests were repeated in the 'bayou' package (Uyeda & Harmon, 2014), which uses a Bayesian mcmc approach to test for multiple optima. A prior that allows one optima change per branch, with each shift randomly assigned in each run, was used in the analyses in 'bayou'. Convergence of optima in 'bayou' was assessed by visual comparison of data within the phenogram, as opposed to the more explicit identification of convergences in 'SURFACE'. The results for 'bayou' optima are displayed as θ which is the average value of the new optima after the shift (Tables 3).

Body mass data were compared to prey-size estimates from Meachen-Samuels & Van Valkenburgh (2009a,b). The correlation among these variables were estimated using phylogenetic generalized least squares (pgls) for both first and last known occurrences as in the previous analyses. The Meachen-Samuels & Van Valkenburgh (2009a,b) prey sizes are divided into small,

mixed and large, which were treated as discrete, quantitative traits with values of one, two and three, respectively, in the analyses. The phylANOVA function in 'phytools' was used to test whether the body masses of felids between the respective groupings were different, after correcting for the phylogeny, whilst also correcting for multiple tests using the Holm correction within the function.

All data, details of the phylogenetic trees and R scripts used in analyses are provided in the Supporting Information.

Results

Modern Felidae

Analysis of the phylogenetic signal in all 39 extant felid body mass values returned a K value less than, but close to, 1 ($K = 0.935$) and statistically significant ($P = 0.001$), suggesting a model similar to Brownian motion and a high degree of phylogenetic signal (Table 1). Lambda (a metric showing the correlation between species relative to that expected under Brownian motion) was also very close to one ($\lambda = 0.881$, $P \ll 0.001$), again supporting strong phylogenetic signal in felid body mass data (Table 1). When alternative models for body mass evolution were compared, a standard Brownian motion model was the best fit for feline body mass evolution out of the five models tested, including a single-optimum OU model (Table 2). Even after carrying out a comparison for multiple optima with 'SURFACE' and 'bayou', the Brownian motion model remained the best for explaining body mass evolution in extant cats (Fig. 1, Table 3).

First occurrence

Analysis of the phylogenetic signal in felid body masses (including all 64 extinct and extant taxa) using first taxonomic occurrence returned a K-value < 1 ($K = 0.530$) and statistically significant ($P = 0.001$), suggesting that the model may not be similar to Brownian motion, but that there is significant phylogenetic signal in the data (Table 1). Lambda was also very close to one ($\lambda = 0.951$, $P \ll 0.001$), again supporting strong

Table 1 Results of analyses of phylogenetic signal for ln body masses (lnBM).

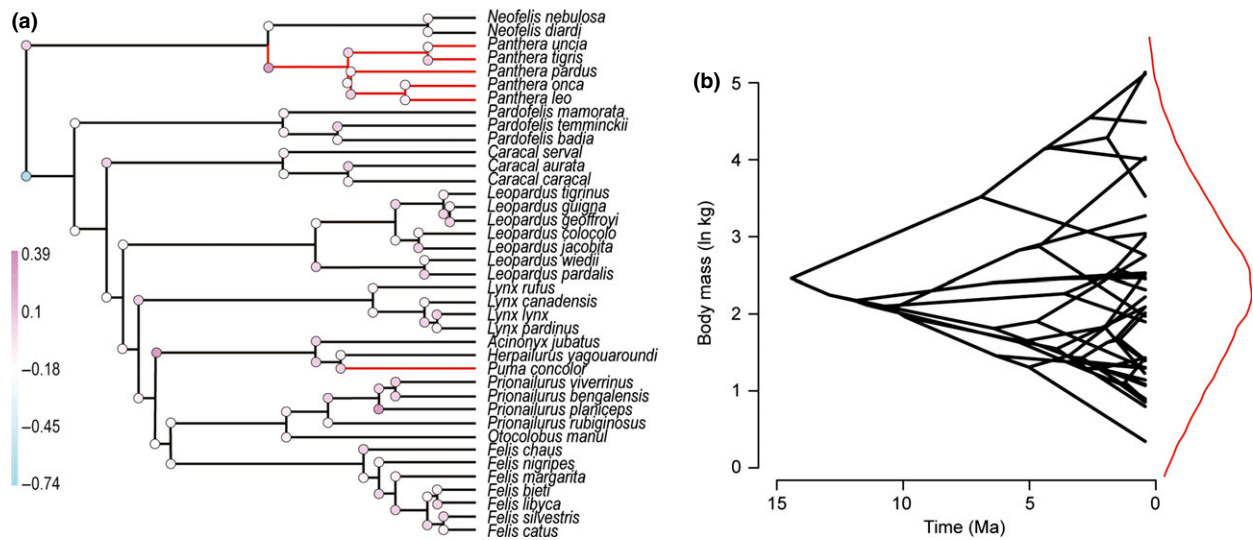|	K	P	λ	Loglikelihood	LogL0	P
lnBM first	0.530	0.001	0.951	−79.0	−121	3.39e-20
lnBM mid	0.846	0.001	0.971	−79.3	−121	6.08e-20
lnBM last	0.912	0.001	0.972	−79.9	−121	1.29e-19
lnBM modern	0.935	0.001	0.882	−47.6	−61.9	8.69e-08

Fig. 1 Phylogeny of only modern felid taxa (modified from Piras *et al.*, 2013) showing the results from 'SURFACE' and 'bayou'. (a) 'SURFACE' and 'bayou' phylogenies with shifts shown. 'SURFACE' shifts shown on the branches (red), whereas 'bayou' rates are shown on the nodes with the colours representing increases and decreases, and the size of the circles showing the probability (all nonsignificant). Note that the multiple OU model shown here has a lower AIC$_c$ than Brownian motion. (b) Phenogram showing distribution of taxa body masses against their phylogeny.

Table 2 Support for each model fit based on AICc values using 'geiger'.

	Brownian	White	Trend	OU	Eb
lnBM first	2.87E-01	3.25E-15	9.63E-02	**5.21E-01**	9.58E-02
lnBM mid	**4.89E-01**	8.15E-19	1.82E-01	1.66E-01	1.63E-01
lnBM last	**4.89E-01**	1.37E-18	1.84E-01	1.64E-01	1.63E-01
lnBM modern	**4.13E-01**	6.69E-07	2.21E-01	2.38E-01	1.27E-01

Brownian = Brownian motion, White = no trend, OU = Ornstein–Uhlenbeck (single optimum), Eb = Early burst.
The bold numbers indicate the most likely model.

phylogenetic signal in felid body mass data (Table 1). When alternative models for body mass evolution were compared, a single-optimum OU model produced the best fit (Table 2). This single body mass optimum occurs around 3.01 (=20.3 kg). Testing for multiple optima using 'SURFACE' found four optima, −58.9 (=2.63 × 10^{-26} kg) and 1.48 (=4.39 kg), 4.22 (=68.0 kg) and 159 (=1.13 × 10^{69} kg), that were better fits than the single OU or Brownian motion models (Fig. 2a), with a phylogenetic half-life of 7.39 Ma. We note the smallest and largest optima are extremely small and extremely large, whereas the two intermediate

Table 3 Summary statistics for parameters for 'bayou' from analysis of the modern felid taxa, first-occurrence and last-occurrence data sets.

	Modern		First occurrence		Last occurrence	
	Mean	SD	Mean	SD	Mean	SD
Log likelihood	−49.0	1.61	−84.7	4.85	−79.1	4.53
Log prior	−47.1	10.6	−54.0	12.1	−56.6	12.1
α	0.0229	0.0463	0.0670	0.701	0.0676	0.715
σ^2	0.1602	0.0521	0.269	0.4333	0.185	0.0609
K	9.66	3.14	9.44	2.99	9.79	3.06
$N\,\theta$	10.7	3.14	10.4	2.99	10.8	3.06
θ_0	2.41	0.578	3.04	0.846	3.26	0.811
θ_{all}	2.22	1.31	2.94	1.44	3.05	1.46

σ^2 is the magnitude of uncorrelated diffusion, α is the rate of adaptation, K is the number of shifts between optima, $N\,\theta$ is the total number of optima, and θ is the optimum value of the process. The θ_0 is the predicted logged mass at the root of the tree, and θ_{all} is the value for all optima. None of the shifts has a posterior probability >0.1 for the modern felids so are not displayed, but the first- and last-occurrence data set shifts are shown in Tables S3 and S4.
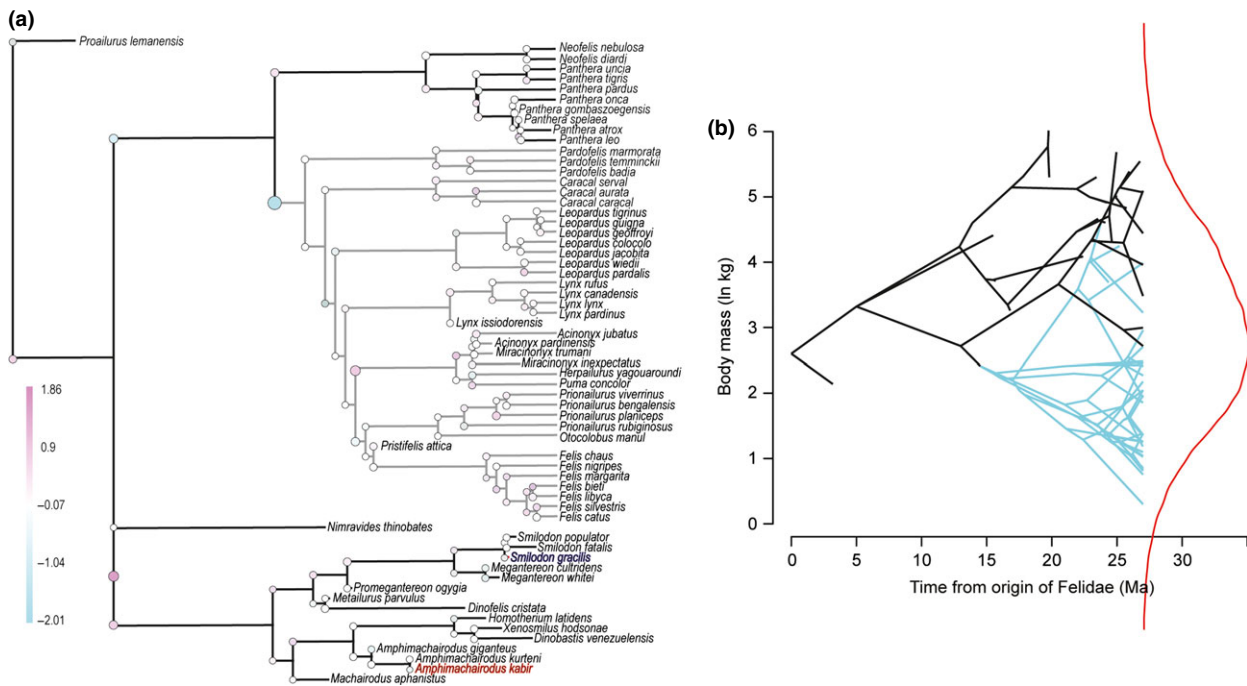
Fig. 2 Phylogeny of all extant and extinct felids using first occurrence dates (modified from Piras *et al.*, 2013) showing the results from 'SURFACE' and 'bayou'. (a) 'SURFACE' and 'bayou' phylogenies with shifts shown. 'SURFACE' shifts shown on the branches (grey, and terminal branches leading to the coloured labels for *Smilodon gracilis* and *Amphimachairodus kabir*), whereas 'bayou' rates are shown on the nodes with the colours representing increases and decreases, and the size of the circled showing the probability (all nonsignificant). (b) Phenogram showing distribution of taxa body masses against their phylogeny for posterior probabilities >0.2 (Table S3). The step down in size occurs at the node leading to the non-*Panthera/Neofelis* felines. When posterior probability was >0.3, a Brownian motion model with no significant changes was recovered.

optima fall within the observed range for both living and extinct cats (Fig. 2b). However, under 'bayou' (Table 3), a Brownian motion model was supported for posterior probabilities >0.3, but for posterior probabilities >0.2, a single shift is detected towards smaller body sizes in the non-*Panthera/Neofelis* felines (Fig. 2c, Table S3).

Mean occurrence

Analysis of the phylogenetic signal in felid body masses (including all 64 extinct and extant taxa) using mean taxonomic occurrence returned a K-value less than, but close to 1 ($K = 0.846$) and statistically significant ($P = 0.001$), suggesting that a model similar to Brownian motion is likely, although closely related species are slightly less similar in body mass than expected based on relationship alone (Table 1). Lambda was also very close to one ($\lambda = 0.971$, $P \ll 0.001$), again supporting strong phylogenetic signal in felid body mass data (Table 1). When alternative models for body mass evolution were compared, a standard Brownian motion model was the best fit for felid body mass evolution out of the five models tested, including a single-optimum OU model (Table 2). However, further exploration of

increasingly complex OU models in 'SURFACE' supported a more parameterized model with six regime shifts (phylogenetic half-life of 3.20 Ma) between two body mass optima: a lower optimum of 1.62 (=5.03 kg), and an upper optimum of 4.59 (=98.9 kg) (Fig. S1). These six evolutionary regime shifts are reconstructed as occurring: in the terminal branch leading to *Proailurus*; between *Proailurus* and all other felids; the base of *Neofelis*; the base of Felinae; the base of the 'Puma' lineage; and the terminal branch leading to *Herpailurus* (*Puma*) *yagouaroundi*. However, analysis of the same data set with 'bayou' again supported a Brownian motion model for body mass evolution (Fig. S1, Table S5).

Last occurrence

Analysis of the phylogenetic signal in felid body mass (including all 64 extinct and extant taxa) using last taxonomic occurrence returned a K value less than, but close to 1 ($K = 0.912$) and statistically significant ($P = 0.001$) suggesting that a model similar to Brownian motion is likely, although closely related species are slightly less similar in body mass than expected based on relationship alone (Table 1). Lambda was also very close

to one ($\lambda = 0.972$, $P \ll 0.001$), again supporting strong phylogenetic signal in felid body mass data (Table 1). When alternative models for body mass evolution were compared, a standard Brownian motion model was the best fit for felid body mass evolution, out of the five models tested, including a single-optimum OU model (Table 2). However, further exploration of increasingly complex OU models in 'SURFACE' supported a more parameterized model with the same six regime shifts (phylogenetic half-life of 3.52 Ma) between two body mass optima as seen in the mean-occurrence results (Fig. 1), but with a slight difference in the magnitudes of the optima: the lower optimum recovered was 1.60 (=4.95 kg), whereas the upper optimum was 4.63 (=103 kg) (Fig. 3a). Similar optima were recovered when the last-occurrence data set was analysed with 'bayou' (Table 3), which returned two major shifts from the initial optima with a decrease in size into the non-*Panthera*/*Neofelis* felines and an increase in size in the *Puma*/*Acinonyx* clade to body masses convergent with the larger felids. These apparent convergences between the optima are similar to those seen in 'SURFACE' (Fig. 3b,c), but do not match the absolute magnitudes (Tables 3 and S4). This is particularly true for the larger optima ($\theta_2 = 3.66$, 38.9 kg) which may be a result of

the presence of the smaller *Herpailurus* taxon being included, which appears to convergently re-evolve small body masses (Fig. 3). This pattern is only recovered for posterior probabilities >0.2 (Table S4), but for posterior probabilities >0.3, a Brownian motion model with no significant changes is recovered.

These two optima entirely distinguish 'small cat' (approximately 5 kg) and 'big cat' (>25 kg) ecomorphs, with no overlap in body mass ranges for species in these two groupings and approximately 5 kg of difference between the largest 'small cat' (Sunda clouded leopard – *Neofelis diardi*) and the smallest 'big cat' (cheetah – *Acinonyx jubatus*) (Supporting Information).

Felinae

For first, mean and last occurrence of Felinae, 'SUR-FACE' returned the two-optima model, whereas 'bayou' finds Brownian motion to be a better fit for all occurrences (Figs S6–S8).

Prey selection

Within the extant felids, there is a significant difference between body masses for each of the prey-size group-
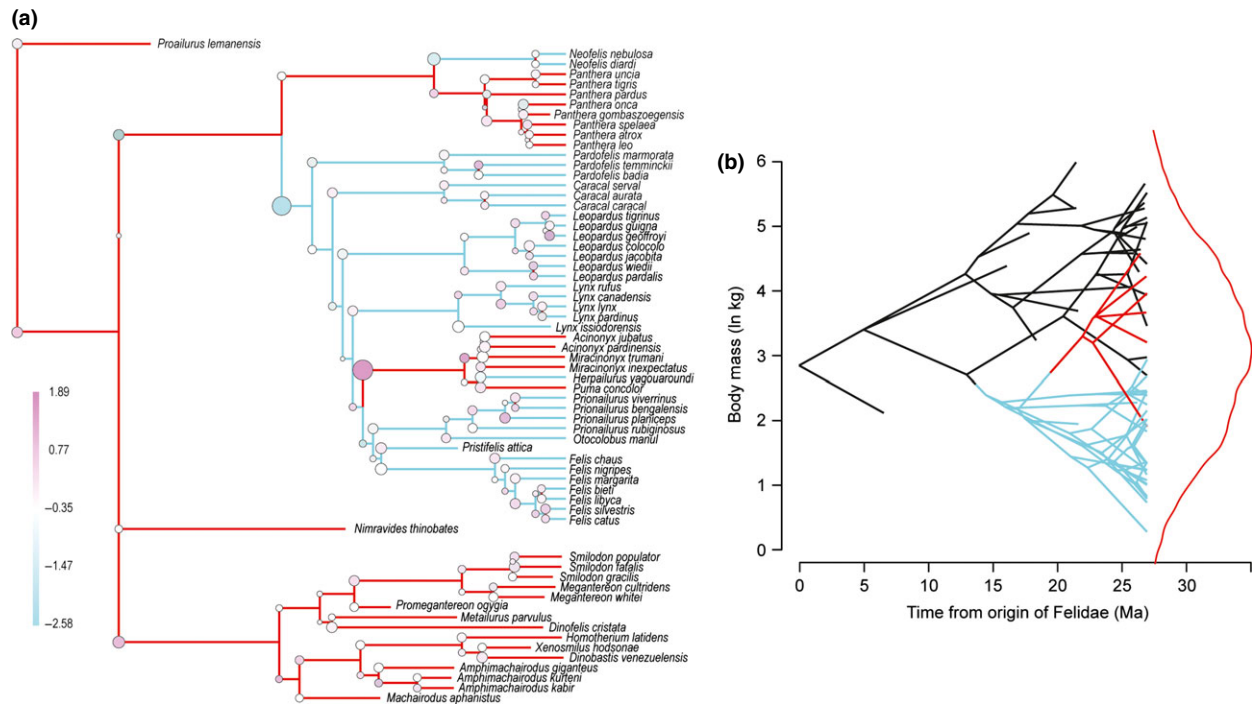

Fig. 3 Phylogeny of all extant and extinct felid taxa using last occurrence dates (modified from Piras *et al.*, 2013) showing the results from 'SURFACE' and 'bayou'. (a) 'SURFACE' and 'bayou' phylogenies with shifts shown. 'SURFACE' shifts shown on the branches (red and blue), whereas 'bayou' rates are shown on the nodes with the colours representing increases and decreases, and the size of the circles showing the probability. (b) Phenogram showing distribution of taxa body masses against their phylogeny for posterior probabilities >0.2 (Table S4). Convergence shows the puma/cheetah lineage mostly being in the large body mass optima, whereas the clouded leopard species converge into the small body mass optima. When posterior probability was >0.3, a Brownian motion model with no significant changes was recovered.

ings ($F = 53.9$, $P = $ 1e-05). Even after correcting for multiple comparisons using the Holm method, there remains significant differences in felid body size among all prey-size groupings (Table S2).

Discussion

Body mass is a trait that has been extensively studied for centuries, both for its relative ease for data collection and for its correspondence to numerous life history and ecological traits, from gestation time to home range size (e.g. du Toit, 1990; McNab, 2002). Previous studies using phylogenetic comparative methods have demonstrated that body mass strongly reflects phylogenetic relationships among taxa, more than almost any other trait (Blomberg *et al.*, 2003) and studies of living taxa often find that body mass evolution follows a Brownian motion model of evolution (Harmon *et al.*, 2010). However, studies incorporating fossils often find stronger support for more complex models of trait evolution (e.g. Finarelli and Goswami, 2013; Raj Pant *et al.*, 2014; Slater 2013).

Felids present an interesting case for the analysis of body mass because it is often suggested that size is the main factor distinguishing different species within this entire clade, with many aspects of felid morphology scaling isometrically with size and most differences in shape among species overwhelmingly due to allometry (i.e. size-related shape change; Davis 1962; Wayne, 1986; Sears *et al.*, 2007; Doube *et al.*, 2009). Our results show that body mass is indeed strongly linked to phylogeny in Felidae; however, the specific pattern reconstructed for body mass evolution in felids is highly dependent on whether extinct taxa are included and what dates are used for the fossils in the phylogeny (Table 1). There are also differences in results stemming from whether multiple-optima models are considered, or which algorithm is used to reconstruct optima (Figs 1–3).

Uyeda & Harmon (2014) recently developed the algorithm 'bayou' and demonstrated that it can produce more realistic optima than those returned by 'SURFACE' (Ingram & Mahler, 2013). In this study, we also find that 'SURFACE' produced optima that are unrealistic for felid body masses (almost as large as Jupiter or as small as an atom of carbon) when run with first occurrence dates in Felidae. This result for 'SURFACE' is likely influenced by short branch lengths leading to variable alpha and sigma values through the tree, or indeed there being a strong selection for big and small cats that have just not obtained their optimal body masses yet (Ingram & Mahler, 2013; T. Ingram, personal communication). It is also interesting that there is a discrepancy between the two methods for the mean occurrence dates, with 'SURFACE' finding two optima that are repeatedly explored, whereas bayou supports a Brownian motion model (Fig. S1). Both methods

concur by finding the same two selective optima, and multiple instances convergence, when last-occurrence data are used in the analyses. That 'SURFACE' finds multiple optima in all analyses, whereas 'bayou' finds them in only one of the three analyses, suggesting that 'bayou' is the more conservative approach of the two. Their correspondence in one analysis and deviation in the other two, however, confuses a straightforward interpretation of body mass evolution in felids, with both Brownian motion and two-optima models receiving some support.

Extant felines cover the majority of the felid clade's total body mass range, but analyses excluding extinct cats consistently supported a Brownian motion model. When extinct felids are added to create either crown Felinae or Felidae, more complex models may become supported. Interestingly, most of the fossil taxa included in the study have large body masses (except for *Proailurus*). Whether this accurately reflects felid evolution or is due to a preservational bias will require further studies, but the wealth of small to medium-sized mammalian fossils suggests the former, particularly as the smallest known felids are, at 1 kg, still relatively large for mammals. The inclusion of fossil felids into the analyses reduced the support for Brownian motion relative to more complex models in some analyses. This effect of fossil taxa on model support may be driven by the preferential extinction of taxa with large body masses. Specifically, previous studies have generally used first-occurrence data rather than mean or last occurrence dates for estimating branch lengths (e.g. Finarelli and Goswami, 2013; Raj Pant *et al.*, 2014). However, there may be some justification for using mean or last occurrence dates in felids due to population-level trends in body mass. For example, within the genus *Smilodon*, there is a trend towards increasing body mass within one species (*fatalis*) from 36 ka to its extinction at 13–14 ka (Meachen *et al.*, 2014). As body mass was taken as an average across specimens, which in some cases span the species' duration for well-represented fossil taxa, this could result in overestimating body mass at the first appearance of a particular taxon (as well as potentially underestimating it for a taxon's last occurrence). Whether this particular effect underlies the differences observed between the analyses of first, mean, and last appearance dates is unknown, but the results are undoubtedly counterintuitive, with analyses using first appearance dates showing greater support for Brownian motion models while those using last appearance dates supporting a two-optima model. The effect of intraspecific trends in body mass may be one possible explanation for this result.

Historically, extant felids have been split into big and small cats with the puma and cheetah convergently evolving large sizes despite being phylogenetically allied to the 'small' cats. The results from analysis with 'SURFACE' and 'bayou' (with last appearance dates only for

the latter) suggest that this traditional grouping is an accurate reflection of felid evolution, not just for extant felids, but the entirety of living and extinct Felidae. Felids possess two distinct and nonoverlapping body mass optima that correspond to small (around 5 kg) and big (>25 kg) cat ecomorphs (Fig. 2). These two groupings reflect strong phylogenetic signal in body mass evolution across felids, whereas there are multiple convergences in the evolution of body mass across cats, and phylogenetic signal in cat body mass appears to be less than has been observed in other clades (Blomberg *et al.* 2003).

Our analyses also refine the current understanding of prey-size preferences across felids. We find that the average preferred prey items in big cats are as large, or larger, than themselves, whereas for the smallest cats, the average prey is smaller than the cat (Supporting Information). Carbone *et al.* (1999) suggested that carnivorans above a approximately 21.5–25 kg threshold have to take prey larger than themselves due to energetic requirements. For extant felids, it has previously been suggested that 'all cats over 25 kg kill large prey, and all cats under 15 kg kill small prey; however, within the body mass range of 15–25 kg, cats may kill only small prey, only large prey, or a mixture of both, to varying degrees, and prey size is not only determined by cat size' (Meachen-Samuels & Van Valkenburgh, 2009a, p. 786). Our results demonstrate that all of the cats that take 'mixed' prey (Carbone *et al.*, 1999, 2007) fall into the small body size optimum but are among the largest individuals within that grouping. Thus, it appears that deviations from a simple relationship between predator and prey body size are driven entirely by large 'small cats'. These large 'small cats' are on the boundary predicted by Carbone *et al.* (2007) where carnivores have to 'adopt behavioural and ecological strategies to minimize the costs as their size approaches the limits imposed by intake rates and hunting costs linked with the size of their prey' (Carbone *et al.*, 2007, p. 0365). This more precise characterization of prey-size preferences across extant felids also improves predications of prey-size choice in extinct taxa.

The two selective optima for felid body mass that we recovered from some of our analyses also broadly reflect previous suggestions of small and large body size optima for mammals as a whole (Alroy, 1998). However, the large body optimum observed for felids is approximately eight times smaller than the large body optimum recovered for Mammalia by Alroy (1998), and indeed is even smaller than the unstable 'medium' body optimum (around 150 kg) recovered in that study. Moreover, despite having at most two selective optima, our analyses show some support for a relatively complex model of body mass evolution across felids. The most primitive felid (*Proailurus*) possessed a small body mass (about 10 kg), and there are three reconstructed shifts to large body masses in felid subclades, as well as three shifts to smaller body masses. These repeated convergences of both small and large body masses throughout felid evolution (Fig. 3) offer a marked contrast with canids which, with the exception of the 'foxes', show a consistent bias towards larger body mass throughout their evolution, as predicted by Cope's Rule (Van Valkenburgh *et al.*, 2004; Finarelli, 2007). It should be noted, however, that the largest canids (about 70 kg) are still smaller than the large body optima of felids, and far smaller than the largest felid body masses attained.

Conclusion

Phylogeny is an important factor underlying body mass evolution within Felidae, but felid body mass evolution is not necessarily simple. Depending on whether or not fossil taxa are included, which algorithm was applied, and whether first, mean or last occurrence dates are used for the extinct taxa, model support shifted from Brownian motion to multiple-optima OU models. For the multiple-optima models, felid body mass evolution was best explained by two optima that were convergently explored by many different clades. These optima correspond to 'big cat' and 'small cat' ecomorphs, and correspond generally to prey choice: 'big cats' consume prey equal to or greater in size than themselves, whereas 'small cats' target prey smaller than themselves. The main exception to this pattern is found among the larger 'small cats', which also take some larger prey. The underlying driver for the observed pattern of two distinct selective optima for felid body mass is unclear, but may be driven by biomechanical constraints related to prey size and prey capture. The extinction of many of the large felids may contribute to the appearance of support for a Brownian motion model of evolution for felid body size when fossil taxa are excluded from analyses, and caution must be used when analyses ignore a clade's past diversity.

References

Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* **280**: 731–734.

Arnold, A.J., Kelly, D.C. & Parker, W.C. 1995. Causality and Cope's rule; evidence from the planktonic foraminifera. *J. Paleontol.* **69**: 203–210.

Blomberg, S.P., Garland, T.J. & Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.

Carbone, C., Mace, G.M., Roberts, S.C. & Macdonald, D.W. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* **402**: 286–288.

Carbone, C., Teacher, A. & Rowcliffe, J.M. 2007. The cost of carnivory. *PLoS Biol.* **5**: e22.

Cope, E.D. 1887. *The Origin of the Fittest*. Appleton, New York, NY.

Davis, D.D. 1962. Allometric relationships in lions versus domestic cats. *Evolution* **16**: 505–514.

Day, L.M. & Jayne, B.C. 2007. Interspecific scaling of the morphology and posture of the limbs during the locomotion of cats (Felidae). *J. Exp. Biol.* **210**: 642–654.

Doube, M., Wiktorowicz-Conroy, A., Christiansen, P., Hutchinson, J.R. & Shefelbine, S. 2009. Three-dimensional geometric analysis of felid limb bone allometry. *PLoS ONE* **4**: e4742.

Finarelli, J.A. 2007. Mechanisms behind active trends in body size evolution of the Canidae (Carnivora: Mammalia). *Am. Nat.* **170**: 876–885.

Finarelli, J.A. & Goswami, A. 2013. Potential pitfalls of reconstructing deep time evolutionary history with only extant data, a case study using the canidae (Mammalia, Carnivora). *Evolution* **67**: 3678–3685.

Gould, S.J. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. *J. Paleontol.* **62**: 319–329.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**: 129–131.

Harmon, L.J., Losos, J.B., Davies, T.J., Gillespie, R.J., Gittleman, J.L., Jennings, W.B. *et al.* 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution* **64**: 2385–2396.

Ingram, T. & Mahler, D.L. 2013. SURFACE: detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise AIC. *Methods Ecol. Evol.* **4**: 416–425.

Johnson, W.E., Eizirik, E., Pecon-Slatter, J., Murphy, W.J., Antunes, A., Teeling, E. *et al.* 2006. The late Miocene radiation of modern Felidae: a genetic assessment. *Science* **311**: 73–77.

Kembel, S.W. 2010. An introduction to the picante package. http://picante.r-forge.r-project.org/picante-intro.pdf.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. *et al.* 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**: 1463–1464.

Macdonald, D.W. & Loveridge, A.J. 2010. *Biology and Conservation of Wild Felids*. Oxford University Press, Oxford, UK.

Martin, L.D., Babiarz, J.P., Naples, V.L. & Hearst, J. 2000. Three ways to be a saber-toothed cat. *Naturwissenschaften* **87**: 41–44.

Mazák, J.H., Christiansen, P. & Kitchener, A.C. 2011. Oldest known pantherine skull and evolution of the tiger. *PLoS ONE* **6**: e25483.

McKenna, M.C. & Bell, S.K. 2000. *Classification of Mammals*. Columbia University Press, New York, USA.

McKinney, M.L. 1986. Ecological causation of heterochrony: a test and implications for evolutionary theory. *Paleobiology* **12**: 282–289.

McNab, B.K. 2002. *The Physiological Ecology of Vertebrates: A View from Energetics*. Cornell University Press, Ithaca, NY.

McShea, D.W. 1994. Mechanisms of large-scale evolutionary trends. *Evolution* **48**: 1747–1763.

Meachen, J.A., O'Keefe, F.R. & Sadleir, R.W. 2014. Evolution in the sabre-tooth cat, *Smilodon fatalis*, in response to Pleistocene climate change. *J. Evol. Biol.* **27**: 714–723.

Meachen-Samuels, J. & Van Valkenburgh, B. 2009a. Craniodental indicators of prey size preference in the Felidae. *Biol. J. Linn. Soc.* **96**: 784–799.

Meachen-Samuels, J. & Van Valkenburgh, B. 2009b. Forelimb indicators of prey-size preference in the Felidae. *J. Morphol.* **270**: 729–744.

Meachen-Samuels, J.A. & Van Valkenburgh, B. 2010. Radiographs reveal exceptional forelimb strength in the sabretooth cat, *Smilodon fatalis*. *PLoS ONE* **5**: e11412.

Novack-Gottshall, P.M. & Lanier, M.A. 2008. Scale-dependence of Cope's rule in body size evolution of Paleozoic brachiopods. *Proc. Natl. Acad. Sci. USA* **105**: 5430–5434.

Peigné, S. 1999. *Proailurus*, l'un des plus anciens Felidae (Carnivora) d'Eurasie: systématique et evolution. *Bull. Soc. Hist. Nat. Toulouse* **135**: 125–134.

Peigné, S., de Bonis, L., Likius, A., Mackaye, H.T., Vignaud, P. & Brunet, M. 2005. A new machairodontine (Carnivora, Felidae) from the Late Miocene hominid locality of TM 266, Toros-Menalla, Chad. *C. R. Palevol* **4**: 243–253.

Piras, P., Maiorino, L., Teresi, L., Meloro, C., Lucci, F., Kotsakis, T. *et al.* 2013. Bite of the cats: Relationships between functional integration and mechanical performance as revealed by mandible geometry. *Syst. Biol.* **62**: 879–900.

R Core Team. 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rothwell, T. 2003. Phylogenetic systematics of North American *Pseudaelurus* (Carnivora: Felidae). *Am. Mus. Novit.* **2403**: 1–64.

Raj Pant, S., Goswami, A. & Finarelli, J.A. 2014. Complex body size trends in the evolution of sloths (Xenarthra: Pilosa). *BMC Evol. Biol.* **14**: 184.

Sears, K.E., Goswami, A., Flynn, J.J. & Niswander, L.A. 2007. The correlated evolution of *Runx2* tandem repeats, transcriptional activity and facial length in Carnivora. *Evol. Dev.* **9**: 555–565.

Slater, G.J. 2013. Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous-Palaeogene boundary. *Methods Ecol. Evol.* **4**: 734–744.

Stanley, S.M. 1973. An explanation for Cope's rule. *Evolution* **27**: 1–26.

Sunquist, M. & Sunquist, F. 2002. *Wild Cats of the World*. University of Chicago Press, Chicago, IL.

du Toit, J.T. 1990. Home range – body mass relations: a field study on African browsing ruminants. *Oecologia* **85**: 301–303.

Tseng, Z.J., Wang, X., Slater, G.J., Takeuchi, G.T., Li, Q., Liu, J. *et al.* 2014. Himalayan fossils of the oldest known pantherine establish ancient origin of big cats. *Proc. R. Soc. Lond. B Biol. Sci.* **281**: 20132686.

Uyeda, J.C. & Harmon, L.J. 2014. A novel Bayesian method for inferring and interpreting the dynamics of adaptive landscapes from phylogenetic comparative data. *Syst. Biol.* **63**: 902–918.

Van Valkenburgh, B., Wang, X. & Damuth, J. 2004. Cope's Rule, hypercarnivory and extinction in North American canids. *Science* **306**: 101–104.

Wayne, R.K. 1986. Cranial morphology of domestic and Wild Canids: the influence of development on morphological change. *Evolution* **40**: 243–261.

Wozencraft, W.C. 2005. Order carnivora. In: *Mammal Species of the World*, 3rd edn. (D.E. Wilson & D.M. Reeder, eds), pp. 532–548. Johns Hopkins University Press, Baltimore, MD.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Phylogeny of Felidae (modified from Piras *et al.*, 2013) with mean occurrence dates for branch lengths showing the results from 'SURFACE' and 'bayou'.

Figure S2 Phylogeny of Felinae (modified from Piras *et al.*, 2013) with first occurrence dates for branch lengths showing the results from 'SURFACE' and 'bayou'.

Figure S3 Phylogeny of Felinae (modified from Piras *et al.*, 2013) with mean occurrence dates for branch lengths showing the results from 'SURFACE' and 'bayou'.

Figure S4 Phylogeny of Felinae (modified from Piras *et al.*, 2013) with last occurrence dates for branch lengths showing the results from 'SURFACE' and 'bayou'.

Table S2 T statistic and *P*-values from analyses using phylANOVA.

Table S3 Branches with posterior probabilities (pp) higher than 0.1 for first occurrence data.

Table S4 Branches with posterior probabilities (pp) higher than 0.1 for last occurrence data.

Table S5 Summary statistics for parameters for 'bayou' from analysis of the mean occurrence dataset.

Table S6 Summary statistics for parameters for 'bayou' from analysis of the Felinae first dataset.

Table S7 Summary statistics for parameters for 'bayou' from analysis of the felinae mid dataset.

Table S8 Summary statistics for parameters for 'bayou' from analysis of the felinae last dataset.

Table S1 Felid species; first, mean and last occurrences; body masses; ln body mass.

Data S1 Felinae last occurrence script.

Data S2 Felinae first occurrence script.

Data S3 Felinae middle-occurrence script.

Data S4 First occurrence script.

Data S5 Last occurrence script.

Data S6 Mean occurrence script.

Data S7 Modern script.

Data S8 phylANOVA.

Data S9 lnBM.

Data S10 lnBM Felinae.

Data S11 lnBM modern.

Data S12 Piras.

Data S13 Piras firstappearance.

Data S14 Piras mid.