POTENTIAL PITFALLS OF RECONSTRUCTING DEEP TIME EVOLUTIONARY HISTORY WITH ONLY EXTANT DATA, A CASE STUDY USING THE CANIDAE (MAMMALIA, CARNIVORA)

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Reconstructing evolutionary patterns and their underlying processes is a central goal in biology. Yet many analyses of deep evolutionary histories assume that data from the fossil record is too incomplete to include, and rely solely on databases of extant taxa. Excluding fossil taxa assumes that character state distributions across living taxa are faithful representations of a clade's entire evolutionary history. Many factors can make this assumption problematic. Fossil taxa do not simply lead-up to extant taxa; they represent now-extinct lineages that can substantially impact interpretations of character evolution for extant groups. Here, we analyze body mass data for extant and fossil canids (dogs, foxes, and relatives) for changes in mean and variance through time. AIC-based model selection recovered distinct models for each of eight canid subgroups. We compared model fit of parameter estimates for (1) extant data alone and (2) extant and fossil data, demonstrating that the latter performs significantly better. Moreover, extant-only analyses result in unrealistically low estimates of ancestral mass. Although fossil data are not always available, reconstructions of deep-time organismal evolution in the absence of deep-time data can be highly inaccurate, and we argue that every effort should be made to include fossil data in macroevolutionary studies.

KEY WORDS: Ancestral state reconstruction, body size, evolutionary rates, fossils.

Accurately reconstructing the evolution of biodiversity is central to predicting potential future character change in light of continued environmental change. Both the tempo and the trajectory of macroevolutionary change are of particular interest, as each helps to inform us about the underlying evolutionary processes. Indeed, the study of evolutionary trends in taxonomic diversity and morphological attributes has a rich history in paleobiology (e.g., Stanley 1973; Gould 1988; McShea 1994; Wagner 1996; Jablonski

1997). Recently studies have tended to rely solely on extant taxa to reconstruct evolutionary trends (e.g., Bininda-Emonds et al. 2007; Monroe and Bokma 2010; Venditti et al. 2011; Nyakatura and Bininda-Emonds 2012), in an attempt to leverage the more complete knowledge of character distributions and more precise understanding of phylogenetic relationships for extant taxa. But this approach assumes that the mode of evolutionary change in a character leaves a detectable signal in the extant representatives of
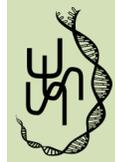
a clade; this may or may not be the case. An additional, but sometimes overlooked, assumption is that the extant taxa are adequate representatives of their clade's entire evolutionary history. This assumption can certainly be a problematic for once speciose, but currently depauperate clades, such as perissodactyls (Janis et al. 1998) or castorid rodents (Flynn and Jacobs 2008). Moreover, this approach completely ignores patterns of character evolution within entirely extinct subclades of larger living groups (e.g., chalicotheres within Perissodactyla or florentiamyid rodents).

Even for groups that are well represented in the modern fauna, accurate reconstruction of deep-time patterns can potentially be hindered if there is no attempt to incorporate fossil data, as extant taxa may be poor proxies of their clade's evolutionary history (Slater et al. 2012). Reconstructions based on select subsets of taxa (including, but not limited to, extant-only data) can be misled by high evolutionary rates (Oakley and Cunningham 2000), non-random extinction (Jablonski and Raup 1995; Jablonski 2008), and/or differential rates or trends that have been masked by extinction of intervening taxa (Ruta et al. 2006; Finarelli 2007). Indeed, simulations and experimental studies indicate that reconstructions of ancestral conditions are improved by incorporating extinct taxa (Huelsenbeck 1991; Graybeal 1998; Wagner 2000; Polly 2001; Finarelli and Flynn 2006; Albert et al. 2009), and that driven trends can bias root state estimates if only extant taxa are considered (Kuhner and Felsenstein 1994; Wagner 1998; Oakley and Cunningham 2000).

Here, we analyze body size evolution in the familiar carnivoran clade Canidae (dogs, jackals, foxes, and their relatives). Canidae has a well-studied and densely sampled fossil record spanning the past 40 million years. Canids are grouped into three subfamilies, the Caninae (to which all extant species belong), and the entirely extinct Borophaginae and Hesperocyoninae. We demonstrate that incorporating body mass data for fossil species fundamentally alters our interpretation of body size evolution. Moreover, as body size is strongly correlated with multiple life history and ecological attributes (Gittleman 1986; Isaac et al. 2005; Carbone et al. 2007), altering our understanding of the evolution of this character could have important consequences for our interpretations of the evolution of life history, ecology, and adaptation to environment for this clade.

Methods

It is now well appreciated that quantifying average character value through time can oversimplify inferences of evolutionary trends (Wagner 1996; Jablonski 1997; Alroy 1998, 2000; Wang 2005). Apparent trends in average phenotype can arise from changes in the mean of the distribution of trait values, changes in the variance, or a combination of the two (Stanley 1973; Gould

1988; McShea 1994). Moreover, true trends in average phenotype can be obscured by changes in the variance of its distribution (Wang 2005). Accurate modeling of evolutionary trends must account for changes in both average phenotype and the variance (Hunt 2006, 2007; Solow and Wang 2008; Venditti et al. 2011). A related, but slightly different, problem concerns estimation of evolutionary rates, or phenotypic change normalized to some measure of elapsed time (e.g., absolute time, branch length, internal node count). Such rates are often employed as descriptive statistics for evolutionary trends, and on the surface, rate estimation seems simple: quantify difference in phenotype and divide by elapsed time (effectively calculating the slope of a plot of phenotype against time). However, this too can conflate the separate impacts of mean and variance (Stanley 1973; Gould 1988; see also Alroy 1998; 2000), potentially obscuring evolutionary patterns and misleading interpretations of underlying mechanisms.

Here we expand on Hunt's (2006, 2007) set of models for a generalized random walk describing evolutionary change in a continuous character for a time series in an evolving lineage. Our re-formulation applies Hunt's framework to a different phylogenetic scale, using canid body sizes (at the species first appearance event [FAE]) as observations in a time series of species occurrences within the clade (see also Sookias et al. 2012). The complete data set of Ln-transformed body sizes then constitutes time-calibrated observations, to which we attempt to fit a changing normal distribution. The log-likelihood for a normal variate with mean (M) and variance (V) is given by

$$\text{Log } L\,(x|\text{Norm}(M,\,V)) \propto$$
$$-\frac{1}{2}\log{[V]} - \frac{(x-M)^2}{(2V)}\,(\text{Edwards}1992). \qquad (1)$$

Allowing M and V to vary as a function of time, we substitute $M(t)$ and $V(t)$ into equation (1), where t is the elapsed time along a branch. From this we can formulate a diverse set of models as specific realizations of this general form. For the present analysis, we consider $M(t)$ and $V(t)$ as linear functions, formulated as:

$$M(t) = \alpha t + \mu_0, \qquad (2a)$$
$$V(t) = \beta t + \sigma_0^2. \qquad (2b)$$

(see Hunt 2006). We note that our symbols in equations (2a) and (2b) differ from previous work. The ancestral mean and variance are given by μ_0 and σ_0^2, respectively. These parameters describe the initial normal distribution of character values among canid species. The terms α and β are linear trend terms, where α quantifies the drift in the mean of the distribution (McShea 1994; Wagner 1996), and β is the Brownian diffusion rate (Felsenstein 1985; Garland et al. 1992). Here, α relates the change in Ln-kg per million years, and β gives the change in (Ln-kg)^2 per million

years. Together α and β describe the how the normal distribution changes from its initial root condition defined by μ_0 and σ_0^2 through time. These four parameters then give the expected shape of the body size distribution at any time (t) during the evolutionary history of the Canidae.

We can then calculate the likelihood of observing any given species' body mass at its FAE. Optimizing the parameters over the set of all observed masses gives the best-fit changing normal distribution through time. With these four parameters, one can represent a Brownian Motion-type model: $\alpha = 0$, $\beta \neq 0$ (such that there no change in mean through time, but variance changes linearly with time; Felsenstein 1985; McShea and Brandon 2010), a driven (or "active") trend: $\alpha \neq 0$, $\beta = 0$ (where the variance remains constant through time, but there is linear drift in the mean) (McShea 1994; Wagner 1996), and generalized or trended, random walks: $\alpha \neq 0$, $\beta \neq 0$ (in which both the mean and the variance change linearly with respect to time; Hunt 2006, 2007).

By estimating ancestral mean and variance, we model an ancestral distribution, with the values for μ_0 and σ_0^2 being established effectively instantaneously in geologic time, and then allow this distribution to evolve over time. In principle, this allows for densely sampled records (taxonomically and temporally) to show the near-zero initial variance that would be expected at a cladogenic event, but also allows for records that are more coarsely sampled or systems that are more quickly evolving to be modeled with an estimated initial state. However, the primary implication of this parameterization of variance involves a fundamentally different treatment of evolutionary stasis (Roopnarine 2001; Hunt 2007). Given our terminology, above, stasis is the special case where α and β both equal 0. That is, an initial distribution is established in a geologically fast interval, and remains invariant through the clade's history. Therefore, in our formulation stasis is not a distinct mode of evolution, but rather a particular realization of a general form of character change.

Finally, we note that $M(t)$ and $V(t)$ need not be linear functions, and future work will explore more complex sets of potential submodels (Hansen 1997; Blomberg et al. 2003; Wang 2005; Harmon et al. 2010; Kolokotrones et al. 2010; Sookias et al. 2012). Parameterization of the various evolutionary patterns is given in Table S1.

We applied this general model structure to a database of body size and appearance data for extinct and extant Canidae (Finarelli 2007, 2008b), with additional fossil data for the Caninae from Tedford et al. (2009). We used a simplified canid phylogeny (Fig. 1), compiled from the paleontological and molecular phylogenies (Wang 1994; Tedford et al. 1995; Wang and Tedford 1996; Wang et al. 1999; Bardeleben et al. 2005; Lindblad-Toh et al. 2005; Tedford et al. 2009). Subgroup membership, appearance events, and body mass data for each species are given in Table S2. Basal groupings (e.g., Basal Borophaginae) are
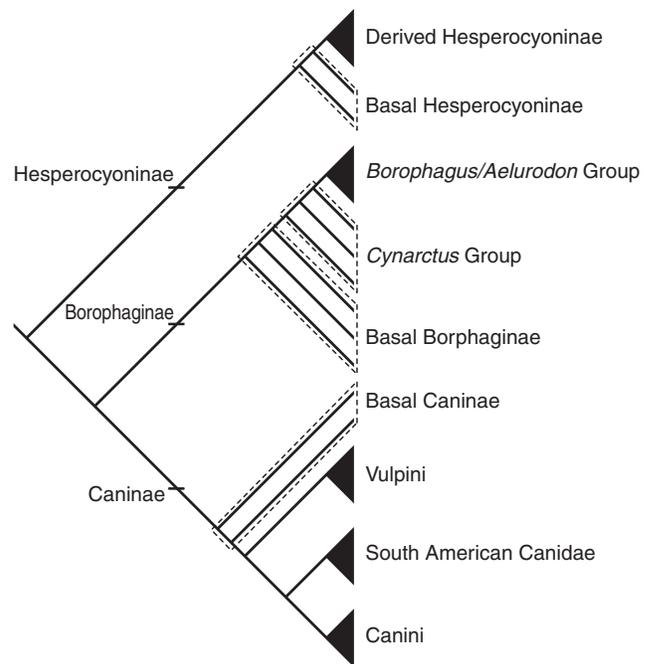
Figure 1. Cladogram of living and extinct Canidae used in this analysis, with subgroups denoted as in Table S2. It is derived from morphological and molecular analyses of extinct and extant canids (Wang 1994; Tedford et al. 1995, 2009; Wang and Tedford 1996; Wang et al. 1999; Bardeleben et al. 2005; Lindblad-Toh et al. 2005) and represents a simplified cladogram following well-supported topologies of these analyses.

paraphyletic groups, which test hypotheses that changes in the mode of body size evolution occurred as apomorphies in derived group. We considered two additional paraphyletic "backbone" groupings spanning basal groups in multiple subfamily clades (see Finarelli and Flynn 2009). Backbone 1 comprised the three basal clades (Basal Hesperocyoninae, Basal Borophaginae, Basal Caninae/Vulpini). Backbone 2 consisted of only Basal Hesperocyoninae and Basal Borophaginae.

Our treatment of canid phylogeny contrasts models of body size evolution among well-supported groups, while simultaneously acknowledging that significant phylogenetic ambiguity exists within these groups (Finarelli and Flynn 2009). Model parameters were estimated for each of the four model types (Table S1), treating the entire Canidae as a single clade with a uniform mode of body size evolution. From this starting point, we evaluated subclade models based on the cladogram in Figure 1. The model with the fewest fitted parameters proposes stasis across the entire canid phylogeny, calculating ancestral mass and variance ($K = 2$, Model 4 in Table S3). More complex model structures and estimating parameters separately for finer phylogenetic groups will potentially describe body size evolution more accurately, but will do so through added model complexity (Finarelli 2008a, 2008b; Finarelli and Flynn 2009). We calculated model likelihoods using

Table 1. Weighted average parameter estimates calculated from Table S4 (see Burnham and Anderson 2002, 2004). Masses and rates are in Ln(kg). Model-averaged parameter estimates.

Taxonomic group	μ_0	σ_0^2	α	β
Canini	0.369	1.00E−07	0.056	0.032
Basal Caninae/Vulpini	0.413	0.221	0.035	0.015
South American Canidae	2.198	4.60E−08	0.020	0.071
Borophaginae *Borophagus*-group	3.038	0.178	0.076	***
Borophaginae *Cynarctus*-group	−0.354	1.00E−07	0.142	0.015
Borophaginae basal	0.396	0.304	0.089	0.031
Derived Hesperocyoninae	1.152	0.000	0.119	0.049
Basal Hesperocyoninae	1.261	0.063	0.120	0.035

the small sample corrected Akaike Information Criterion (AIC$_c$; Hurvich and Tsai 1989; Burnham and Anderson 2002), given by

$$\text{Log } L(\text{Model}) \propto -\frac{1}{2}\left(\text{AIC}_c(\text{Model}) - \text{Min AIC}_c\right) \qquad (3)$$

(Burnham and Anderson 2002), where AIC$_c$(Model) is the AIC$_c$ score of the model under consideration and MinAIC$_c$ is the minimum AIC$_c$ score across all models. These likelihoods calculate the fit of the model to the body size data, incorporating a penalty for increased model complexity (Burnham and Anderson 2002). We considered a parameter-corrected log-likelihood difference of 2 as the cutoff for significant difference in support between models (Edwards 1992; Royall 1997; Wagner et al. 2006).

Total model parameterization is the sum of the submodel parameters fit to each canid subgroup. For example, for a model proposing Brownian Motion in the subfamilies Caninae and Hesperocyoninae and evolutionary stasis in the Borophaginae (Model 22 in Table S3), the total number of parameters would be $3 + 3 + 2 = 8$ parameters. A final model modification involved combination of estimated values for α (trend in mean value; see Finarelli and Flynn 2009), estimating a single drift rate for the mean (active trend and trended, random walk models) across groups. This can potentially simplify models, at the expense of slightly lower fit to the data (Burnham and Anderson 2002; Finarelli and Flynn 2009). We evaluated a total of 300 models (Table S3) using the Solver tool in MS Excel 2010 (Redmond, WA).

Results

Ten of the 300 evaluated models fell within 2LnL of the best score (Table S4). There is broad agreement in significant aspects of canid body size evolution across this set of models. All 10 models agree that all of the canid subgroups needed to be modeled separately, which likely indicates that the cladogram in Figure 1 is oversimplified and that better phylogenies and larger fossil sample sizes may ultimately support even more complex body size evolution in canids. However, with respect to even such a coarse-grained phylogenetic hypothesis, we can infer a complexity in canid body size evolution that would be impossible to recover from any single time slice, fossil, or recent.

Among the optimal models, fully trended, generalized random walks are most commonly supported (Table S4), demonstrating that both variance and mean are critical parameters for reconstructing body size evolution. Brownian Motion models and stasis are generally not supported: stasis is excluded from the set of optimal models, whereas Brownian Motion is supported in some models for South American canids (with trended walks supported in the other models). Therefore, there is no unambiguous support for diffusive evolution of body size in any canid subgroup. These results may appear to be at odds with Hunt (2007), who found directional models (i.e., $\alpha \neq 0$ in our terminology) to be of minor importance relative to Brownian Motion and stasis. However, that study examined character evolution at a temporal and phylogenetic scale that was far larger than this analysis, and Hunt (2007) noted that body size traits were far more likely than shape traits to exhibit directional trends through time.

Model-averaged parameter estimates (Table 1) were calculated by multiplying the parameter estimates for each of the 10 optimal models by their normalized likelihoods (Table S4). The weighted average parameter estimates demonstrate that the extinct Borophaginae and Hesperocyoninae are defined by substantial drift rates for mean body size (α), indicating "active trends" (McShea 1994; Wagner 1996) of increasing body size through time in all subgroups (Wang 1994; Wang et al. 1999; Van Valkenburgh et al. 2004; Finarelli and Flynn 2006; Finarelli 2007). Within the Caninae, fundamental differences exist in the mode of body size evolution among groups. South American canids and the Vulpini show lower magnitude estimates for α than do the Canini, indicating stronger drift in mean body size for dogs and wolves than in true foxes and endemic South American dogs.

Furthermore, estimated parameters derived from extant taxa alone do not fit observations in the fossil records of either the entire Canidae (including the extinct subfamilies) or just fossil members of the, Caninae. We estimated the parameters for a Brownian Motion model from extant canids, effectively

Table 2. Comparison of Brownian Motion models for the sample of all Caninae species (fossil and extant) and all species in Canidae (fossil and extant) with estimates derived from either from all the data in the sample or from extant taxa only. Log-likelihood differences are substantial in both cases. Masses and rates are in Ln(kg).

Model fit to:	Fossil + Extant Caninae	Fossil + Extant Caninae	Fossil + Extant Canidae	Fossil + Extant Canidae
Parameter estimates derived from:	Fossil + Extant Caninae	Extant Caninae only	Fossil + Extant Canidae	Extant Caninae only
Ancestral mass (μ_0)	2.038	1.739	2.078	1.739
Ancestral variance (σ_0)	1.604	0.692	1.729	0.692
Evolutionary rate (β)	−0.020	0	−0.020	0
LnL	−38.631	−47.200	−100.253	−130.819
ΔLnL		8.569		30.566

simulating an analysis of living taxa only. We compared model fit of all data (fossil and extant) using extant-only parameter estimates to the fit of a model using parameters estimated from all of the data, essentially comparing how well an extant-only data set represents the entire history of the Candiae. We performed this comparison for both the Caninae and for the entire Canidae (Table 2). Estimates derived from all of the data showed significantly better fit to the total data set. More importantly, estimates derived from living taxa only underestimate ancestral masses by more than 30% in both cases (Table 2 and Fig. S1). This implies that mean body size for extant canids is substantially smaller than has been typical throughout canid evolutionary history, agreeing with a previous analysis that showed a substantial, but relatively recent, diversification of small-bodied "foxes" (Finarelli 2007).

Discussion

Increasingly, attempts have been made to reconstruct deep time evolutionary patterns from extant taxa, taking advantage of a growing number of character databases and large-scale phylogenies (e.g., Bininda-Emonds et al. 2007; Venditti et al. 2011; Nyakatura and Bininda-Emonds 2012). In general, incorporating better-resolved and more accurate phylogenies (e.g., Bininda-Emonds et al. 2007), in conjunction with the wealth of character data available for extant taxa (e.g., Ernest 2003; Smith et al. 2003) should improve reconstructions of character histories. However, we would urge caution when reconstructing deep-time patterns solely from extant taxa. Excluding fossil data can be problematic, as several important factors (e.g., differential extinction, rate heterogeneity across time, or among clades) cannot be precisely incorporated into evolutionary models without fossil data. This can mislead inferences of evolutionary processes. For example, the effects of the Pleistocene megafaunal extinction drastically altered mammalian body size distributions (Lyons et al. 2004), but this cannot be accurately estimated without fossil taxa. Therefore, reconstruction of even such a relatively recent pattern could be inaccurate if based exclusively on extant taxa. Even if the pattern of an evolutionary trend were known (or suspected), it

would not be possible to infer an underlying mechanism without fossil data (Hunt 2012; Slater et al. 2012). Differentiating among "passive" trends of unbiased diffusion near a boundary constraint, or "active" trends brought about by either biased production or differential extinction of phenotypes (Stanley 1973; McShea 1994; Wagner 1996; Finarelli 2007) requires reference to the fossil record.

As noted earlier, analyses relying on the extant record do so, in large part, to leverage a far more precise understanding of phylogenetic relationships among living species (e.g., Bininda-Emonds et al. 2007; Venditti et al. 2011). Indeed for the order Carnivora, recent molecular phylogenies have radically changed our understanding of interrelationships (Flynn et al. 2005; Gaubert and Cordeiro-Estrela 2006; Sato et al. 2009; Yu et al. 2011). Unfortunately, phylogenetic analyses integrating fossil taxa, known only for morphological data, with molecular sequence data for extant taxa are rare for the Carnivora (Finarelli 2008c). A complete species-level phylogeny is not yet available for the Canidae, and the simplified canid phylogeny in Figure 1 represents a conservative estimate of interrelatedness. But the lack of a resolved phylogeny does not preclude analyses of evolutionary patterns. A well-sampled fossil record, as exists for this clade (Wang 1994; Wang et al. 1999; Finarelli 2007, 2008b; Tedford et al. 2009), can be used to reconstruct evolutionary trends and to estimate rates using time series approaches similar to what we present here (Hunt 2007; Sookias et al. 2012).

Our analysis points to a decidedly complex character history for body size in the Canidae. A single set of parameter estimates does not adequately describe body size distributions observed in both the past and present; reconstructing deep-time trends in canid body size evolution requires incorporating body mass estimates for fossil dogs. We recover distinct evolutionary patterns for each of the examined subgroups. Moreover, estimates made when using only extant members of this clade underestimate the complexity of body size evolution in this family, and produce estimates of ancestral masses that are not in accord with observations in the fossil record. Although this is interest with respect to the evolution of the Canidae in particular (e.g., Van Valkenburgh et al.

2004), we believe that canid body size provides more generally applicable example of the impact fossil taxa can have on inferences of evolutionary processes. Fossil canids are not described by any distribution of body sizes that fits their extant relatives, and their inclusion has a significant impact on inferences of the evolution of this character (Oakley and Cunningham 2000; Finarelli and Flynn 2006; Smaers et al. 2012). These results support those of Slater et al. (2012), who found that even modest amounts of fossil data were able to substantially alter estimates of ancestral body mass for caniform carnivorans. For these reasons, wholesale exclusion of fossil data based on incompleteness/paucity of data should be viewed with caution. Extant and fossil data, in addition to ongoing efforts to generate better-resolved, comprehensive phylogenies (e.g., Bininda-Emonds et al. 2007) will be necessary to understand the biology of both extinct and living clades.

This is not to say that fossil data constitute a "magic bullet," rendering analyses of character evolution complete and correct. There are clades with poor fossil records (e.g., bats, Czaplewski et al. 2008), and characters of interest that cannot be reconstructed easily from fossil data (e.g., home range size; Ernest 2003). However, just as the lack of molecular sequence data for the vast majority of extinct taxa (which comprise the vast majority of variation in organismal biology) cannot be considered a valid reason to ignore molecular sequence data in evolutionary analyses, difficult cases in the fossil record do not justify summary dismissal of all fossil data. Rather, data from the fossil record, particularly with respect to temporal distributions, taxonomic diversity and morphologic disparity, should be incorporated into analyses when possible.

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

Figure S1. Histograms with cumulative percentage curves for canid body sizes: all canid taxa (top) and extant canid taxa (bottom).
Table S1. Parameterization of the model structures examined in this analysis.
Table S2. Mass and appearance event data for the 163 canid species considered in the analyses.
Table S3. Model description, parameterization, and AICc/log-likelihood scores for the 300 examined models.
Table S4. Summary of model likelihoods and parameter estimates for the 11 models within $2\text{Ln}L$ of the optimal score.