



Using phylogenetic comparative methods to gain insight into the evolution of social complexity

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Abstract

Social complexity can have important evolutionary implications, and phylogenetic comparative methods have long been used as a way to assess interspecific support for hypotheses on the subject. Statistical approaches for conducting such analyses have come a long way in the last few decades, and it is now possible to use comparative data to ask sophisticated questions about the evolution of complex phenotypes while taking also uncertainty in the phylogeny into account. Here, we illustrate these advances by applying a phylogenetic analysis of covariance to two data sets addressing the evolution of social complexity in primates. First, we find that social complexity (as inferred by group size) is predicted by whether a species is diurnal and terrestrial. Second, we find that social complexity (as inferred by social organization) has increased over evolutionary time and can impact trait evolution. Particularly, we find that baculum length has been growing with body size in dispersed, pair-living and, more weakly, multi-male species, becoming relatively smaller and more variable in aggregations that are more socially stable.

Significance statement

Sociality poses a particular challenge for interspecific analyses because of the many ways that its intrinsic complexity can be coded into statistical variables and models. However, with methods that incorporate phylogenies and nuanced inferences about underlying evolutionary processes, even coarse measures of social complexity can offer valuable insights in the study of behavioral trends through time. Exploring two interspecific data sets on primates, we show how simple measures of sociality, either coded as continuous or categorical variables, can be used to revisit latent evolutionary hypotheses while revealing new pieces of information that become available thanks to the added complexity of novel phylogenetic comparative methods. One example reveals that larger and more variable groups are associated with shifts in habitat and activity patterns, while the other reveals that baculum evolution might be influenced by the increasing social stability of primate aggregations.

Keywords Analysis of covariance · Evolution · Group size · Social organization · Phylogenetic comparative method · Primates

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Introduction

Phylogenies and interspecific analyses have long been important to the study of social complexity, both in uncovering general patterns and in inferring phenotypic evolution. For example, Dunbar's (1993) social brain hypothesis resulted from a comparative study showing a strong interspecific relationship between average neocortex size and group size in primates, confirmed by a phylogenetic analysis (Barton 1993). This relationship provided the initial insight that evolutionary increases in primate brain size were linked to the intellectual demands of engaging in sophisticated social relationships with other members of increasingly large social groups (Dunbar 1993). Similarly, phylogenetic comparative analyses of rodents (Pellis and Iwaniuk 1999), ungulates

(Shultz and Dunbar 2006), cichlid fish (Gonzalez-Voyer et al. 2009), social insects (Danforth 2002; Kocher and Paxton 2014), and many other species shed light on the evolution of social structures and their underlying mechanisms (e.g., cognition: MacLean et al. 2012). In recent years, statistical approaches for examining interspecific data in a phylogenetic context have become highly sophisticated and easy to apply (e.g., see Garamszegi 2014). With modern phylogenetic comparative methods, we have easy access to a wide range of tools to infer how social behavior evolved. In this paper, we review some of the benefits of applying phylogenetic comparative methods in studies of sociality and its implications on trait evolution, illustrating the main ideas through two empirical examples.

Despite the many inherent problems with defining and measuring social complexity, even coarse measures of social behavior applied in a comparative and phylogenetic context can be helpful in identifying key factors guiding social evolution and its underlying mechanisms. For example, a simple count of group size may not distinguish the tremendous complexity of a social insect colony (with social castes and division of labor: Beshers and Fewell 2001) from the relatively uniform behavior of a school of fish or swarm of locusts (Sumpter et al. 2008), and may not capture the critical variation in brain size that may drive differences in social complexity (e.g., Kverková et al. 2018). Nevertheless, group size was the primary metric underlying the insights from Dunbar's social brain hypothesis analysis (Dunbar 1993). Other authors have also successfully used categorical variables as descriptors of social complexity (Cheverud et al. 1985; Shultz and Dunbar 2006; Pérez-Barbería et al. 2007; Fuentes-González and Muñoz-Durán 2017). Again, although social organization and mating system may not precisely reflect all elements of social complexity, they are sufficiently linked to complexity that these analyses can offer insights that are particularly useful in terms of generating new hypotheses. More nuanced measures such as the degree of phenotypic differentiation within social groups (Danforth 2002; Kocher and Paxton 2014) or the degree of male-female association (Pellis and Iwaniuk 1999) have also been helpful in gathering insights into the evolution of social complexity. Crude measures may be particularly useful when the primary goal of a comparative analysis is to generate hypotheses for future studies in which social complexity can be more carefully defined.

Phylogenetic comparative methods

As pointed out in the mid 1980s (Felsenstein 1985) and explained in subsequent work (e.g., see reviews by O'Meara 2012; Pennell and Harmon 2013; Martins and Fuentes-González 2018), phylogenetic comparative methods are an important component of any statistical analysis of data

collected from more than two species, whether or not an explicit evolutionary question is being asked. Interspecific data regularly violate the basic assumptions of most parametric statistical tests, such as independence and homoscedasticity. At a very minimum, we need to incorporate phylogenies to correct these statistical problems when estimating parameters or testing hypotheses with comparative data. Incorporating phylogenies can improve the precision of statistical estimates (Rohlf 2006) and offers historical insights that cannot be obtained in other ways (Hansen 2014).

Phylogenetic comparative methods have come a long way since the 1980s and can now handle complex questions, sophisticated inferences, and inaccurate phylogenetic information. Starting with the first advance (i.e., complex questions), for example, complex regression and model-fitting approaches have been developed to incorporate phylogenies with virtually any sort of data or question, including complex link functions (Hadfield and Nakagawa 2010), path analysis (von von Hardenberg and Gonzalez-Voyer 2013; Gonzalez-Voyer and von Hardenberg 2014), and multivariate approaches (Revell 2009). Following up with the second advance (i.e., sophisticated inferences), researchers have developed statistical approaches to infer increasingly complex aspects of the underlying evolutionary process, including different forms of selection (Beaulieu et al. 2012) and evolutionary rates (O'Meara et al. 2006). Finally, on the third advance (i.e., inaccurate phylogenetic information), modern phylogenetic approaches offer creative ways to incorporate realistic levels of information about the phylogeny. In particular, Bayesian and Markov-Chain-Monte-Carlo (MCMC) approaches now offer powerful ways to manage uncertainty in the available phylogenetic information (e.g., Huelsenbeck and Rannala 2003; Ronquist 2004; Pagel and Meade 2006). By allowing much greater flexibility in terms of data and question (first advance), by combining questions about trait relationships with questions about evolutionary rates (second advance), and by incorporating phylogenetic uncertainty (third advance), modern phylogenetic comparative methods can model a wide range of evolutionary scenarios.

Modern approaches lean towards integrating these recent advances in the analysis of interspecific data (e.g., Eastman et al. 2011; Beaulieu et al. 2012; de Villemereuil et al. 2012). A good example of this is the phylogenetic ANCOVA with unequal evolutionary rates (PANCova: Fuentes-González et al. 2016; Fuentes-González 2018), an approach that combines all three of them. At the simplest level, it is an ANCOVA that combines different sorts of interspecific measures by testing whether the relationship between two continuous variables (e.g., brain size and body size) depends on the evolution of a third, categorical trait (e.g., diet). In an important extension, however, the model also infers whether evolution of that third trait is associated with a change in the rate of phenotypic evolution. This test for a burst or shrinkage of phenotypic

radiation offers important new insights into the underlying evolutionary process. Finally, with a Bayesian extension (Fuentes-González 2018), PANCova also incorporates uncertainty in parameter estimation and phylogeny, as well as facilitating the process of model selection. The Bayesian approach is especially useful for the study of social complexity or similar cases when the measures are inherently complex (e.g., with multi-state categorical traits) (Kruschke and Liddell 2018), or when not enough is known about the underlying microevolutionary process to identify appropriate assumptions (e.g., Brownian Motion, Ornstein-Uhlenbeck). The Bayesian PANCova samples widely across complex parameter spaces and possible assumptions, estimating the probability of each scenario given the data and offering reasonable ways to choose among them. Below, we apply the Bayesian PANCova to two primate examples, illustrating how simple measures associated with social complexity, defined as both continuous (Example 1) and categorical (Example 2) measures, can help to identify key factors in social evolution.

Example 1. Habitat and activity patterns predict group size: Social complexity as a continuous response

Often, as in Dunbar (1993), we are trying to explain the evolution of social complexity, determining how much of the interspecific variation in our measures of sociality can be explained by phylogeny, habitat, body size, or activity levels. For example, in an overview of phylogenetic comparative methods, Nunn and Barton (2001) found that larger primates form larger groups but that this relationship disappeared when phylogeny was taken into account using Felsenstein's (1985) independent contrasts. Taking a closer look at the data, Nunn and Barton (2001) suggested that without a phylogenetic context, the relationship between body size and group size was exaggerated by differences between nocturnal primates (small and solitary) and diurnal primates (larger and forming larger groups). Their suggestion was based on a huge literature on the complex interspecific relationship between body size, group size, and lifestyle in primates (e.g., see review by Terborgh and Janson 1986). In essence, Nunn and Barton (2001) pointed out that the interspecific relationship between body size and group size was the result of a difference between a group of data points representing closely related nocturnal primates which avoid food competition and predation by being both small and cryptic, and a second group of data points representing diurnal primates that avoid predators by living high in trees or by forming larger social groups that cooperate in anti-predator vigilance. A simple Felsenstein's (1985) contrast analysis rescaled the variables so that the large difference between these two clades was less exaggerated (in the re-scaling, the two clouds of points were now super-imposed on each other), and the relationship between body size and group size was obscured. Nunn and Barton (2001) thus crafted an ad hoc approach, first estimating the evolutionary increases in body mass and group size

associated with transitions to diurnal and terrestrial lifestyles, and then applying separate sign and *t* tests to show that increases in each trait were significantly larger than expected by chance alone.

The question underlying this example is whether body size predicts group size across primates, once we have taken into account whether they are nocturnal or diurnal, arboreal or terrestrial. In statistical terms, our first example is of social complexity measured in terms of group size and treated as a response variable (y) in a multiple regression. With older phylogenetic comparative methods, it was difficult to look for a relationship between group size (y) and body size (z) while also incorporating information on activity patterns and lifestyles (x); hence, Nunn and Barton (2001) applied a combination of independent contrasts, sign, and *t* tests. However, with PANCova (Fuentes-González et al. 2016), we can fit a more complex model that asks not only whether evolutionary changes in group size (y) and body size (z) were separately associated with shifts in habitat and activity (x), but also whether shifts in habitat and lifestyle were accompanied by changes in the scaling relationship between body mass and group size. By considering these simultaneously, we can infer trait interactions and their underlying evolutionary processes more precisely.

Modern phylogenetic comparative analyses offer many other insights into the underlying evolutionary process. For example, Schultz et al. (2011) used Bayesian comparative estimates of transition rates to infer the temporal order of evolutionary shifts, finding strong support for a model in which primates evolve from a solitary and nocturnal lifestyle to a social and diurnal one, with single-male and pair-living groups forming only afterwards. We can use estimates of evolutionary rates also to generate new hypotheses. For example, the evolution of diurnal and terrestrial lifestyles may have opened up a broad range of new ecological and behavioral opportunities, perhaps leading to a burst of phenotypic diversification including dramatic changes in group size. These new lifestyles may also have imposed new constraints on group size, leading different primate species to maintain similar group sizes in a shrinkage of phenotypic diversification. One of the strengths of PANCova is that it combines estimates of evolutionary rates with estimates of the scaling relationships above. Using PANCova, in addition to asking about the relationship between body size and group size, we ask whether shifts to diurnal and terrestrial lifestyles were accompanied by dramatic increases or decreases in the rate at which group size evolved, gaining additional insight into the evolutionary mechanisms involved in these shifts.

Methods

Fitting the PANCova model requires phenotypic data and a phylogeny. We used measures of 101 species compiled from

the literature by Nunn and Barton (2001), supplemented with measures for nocturnal primates (Nunn and van Schaik 2002). Measures of group size consist of counts (described in more detail in Nunn and Barton 2000), and measures of body mass (in kg) are restricted to females in order to minimize confounding contributions of sexually dimorphic species (Smith and Jungers 1997). Both measures were log-transformed following the original work of Nunn and Barton (2001). To these data, we added a set of 1000 plausible phylogenies from version 3 of *10kTrees*, a project that offers primate phylogenies based on currently available molecular information and reflecting realistic levels of uncertainty about topology and branch lengths (Arnold et al. 2010). The trees derive from 11 mitochondrial and six autosomal genes analyzed under Bayesian inference, and are dated using mean molecular branch lengths and six fossil calibration points. One species, *Tarsius tarsier*, was not present in the phylogenies. We placed it in the same phylogenetic location as *T. dentatus* (not present in the dataset) as a single clade representative of the *T. tarsier*-complex, based on additional information from Kamagi et al. (2014).

To these data, we applied a Bayesian version of PANCOVA (Fuentes-González et al. 2016; Fuentes-González 2018). In order to estimate changes in the rate of phenotypic evolution, PANCOVA requires information on the ancestral states of the categorical trait (nocturnal-arboreal, diurnal-arboreal, or diurnal-terrestrial) throughout the phylogeny. Instead of fixing these, we used stochastic character mapping (Nielsen 2002; Huelsenbeck et al. 2003) to sample multiple descriptions of character state historical patterns on phylogenies, proportional to their posterior probability. Currently, there are several options available that implement this technique (Bollback 2006; Maddison and Maddison 2011; Revell 2012), making it readily accessible for different user preferences. For illustrative purposes, and in order to gain some insights on the different implementations, we use two of them here (one for each example). For this example, we used stochastic character mapping as implemented in the package *phytools* (Revell 2012) for R (R Development Core Team 2016). We used a fixed transition matrix of character states (Q, with three states for this example) with equal rates and a flat prior for the root of the tree. For each tree, we simulated 10 stochastic maps, producing a distribution of 10,000 trees and mappings that were subsequently sampled to produce an empirical prior with 100 historical descriptions of equal probability: $V \sim \Pi(\xi)$, where V represents the phylogenetic covariance due to common ancestry and Π is any relevant distribution with parameters ξ (de Villemereuil et al. 2012), reflecting the collection of trees and mappings. We integrated the PANCOVA estimates over this distribution in order to incorporate the uncertainty on the topology, branch lengths, and evolutionary history of primate activity patterns and habitat.

Bayesian statistics provide a natural way of incorporating identified sources of uncertainty through the use of prior

distributions. For regression coefficients, we used diffuse conjugate univariate normal priors: $\beta \sim N(0, 10^6)$; for parameters that do not have direct equivalents to observed measures, diffuse priors should in general have a small effect on the posterior distribution (Hoff 2009; Blomberg et al. 2012; Kruschke and Liddell 2018). For evolutionary rates, we also used diffuse priors through uniform distributions on the inverse of variance parameters: $\gamma^{-1} \sim U(0, 100)$, reflecting the common practice in Bayesian statistics of parameterizing the variance in terms of precision (Gelman 2006). A phylogenetic signal parameter (λ) can be used in order to determine to what extent the studied pattern is correlated with evolutionary relationships among species (Pagel 1999; Freckleton et al. 2002). A uniform distribution can be used to specify a prior for this parameter: $\lambda \sim U(0, 1)$; the bound between zero and one applies when using ultrametric trees scaled to a height of one (de Villemereuil et al. 2012). The use of the phylogenetic signal parameter also facilitates the task of model comparison with regard of how the studied pattern is influenced by historical effects. Instead of choosing between a simple Brownian motion model of phenotypic evolution, an ahistorical model in which phylogeny has no impact, and the phylogenetic signal model described above, we apply a mixture model to sample the alternatives using a hyperprior of equal probability for each of them. Under this approach, model selection uncertainty on the resulting parameters can be easily accounted for by using Bayesian model averaging.

Using the PANCOVA estimates, shifts in directional trends and phenotypic relationships were explored using the posterior distribution of regression coefficients. In particular, we used credible ranges defined as the 95% highest density interval (Kruschke and Liddell 2018), and posterior probabilities (pp) of parameter values defined by the area under the probability density function that falls under a particular range (de Villemereuil et al. 2012). For regression coefficients, these areas were fundamentally determined by zero (i.e., below or above zero). For multiple comparisons, we obtained credible ranges and posterior probabilities of the differences among regression coefficients, which are computable from the joint distribution across the parameter space (Kruschke and Liddell 2018). Similarly, shifts in phenotypic diversification were tested using the posterior distributions of the differences among evolutionary rates. Credible ranges and posterior probabilities obtained from these distributions were informative of which rates were larger or smaller than others.

To obtain these estimates, we ran three chains for a total of 250,000 generations, without thinning (Link and Eaton 2012). We used 1,000 steps to tune the samplers and excluded the first 25,000 generations as burn-in. The chains were diagnosed by evaluating trace plots, computing effective sample sizes (N_e), and applying stationarity and half-width tests (Heideberger and Welch 1981, 1983) with $\alpha = 0.05$ and $\varepsilon = 0.1$. The R packages *stats*, *graphics*, and *coda* (Plummer et al. 2006) were

used for these diagnostics. The posterior distributions were approximated through MCMC algorithms implemented in JAGS Version 4.2.0 (Plummer 2003) using the scripts presented by Fuentes-González (2018) for R using the package rjags (Plummer 2016). These algorithms include Metropolis-Hastings, Gibbs, and slice samplers, all of which should, in theory, approach the targeted posterior distribution under a large number of generations.

Results

We found that nocturnal primates (black squares in Fig. 1a) have smaller group sizes than do diurnal-arboreal species (red circles in Fig. 1a). This was reflected in y-intercepts estimated by the PANCova model (Table 1), which was 2.0 individuals/group for nocturnal primates (converting $b_{INA} = 0.3$ from a \log_{10} scale) but closer to 5.2 individuals/group for diurnal-arboreal species ($b_{IDA} = 0.5$ larger than b_{INA}). Diurnal-terrestrial primates (blue triangles in Fig. 1a) also had larger groups (4.5 animals/group per 1 kg in female mass; $b_{IDT} = 0.4$) than did the nocturnal species, although this difference in intercept-estimates was somewhat less credible (estimate ranges overlap in Table 1). Importantly, the difference between estimated group sizes for diurnal vs nocturnal primates was apparent only for large-bodied primates (> 1 kg; Fig. 1b), in part because the diurnal-terrestrial species are the only ones for which the scaling relationship between group size and body size credibly deviated from the rest (Fig. 1b; b_{SDT} in Table 1).

The relationship between group size and body size was quite small for both nocturnal primates ($b_{SNA} = -0.1$, Table 1) and for diurnal-arboreal species ($b_{SDA} + b_{SNA} = 0.1$, range = $-0.16, 0.33$). This difference in scaling effects also had an impact on the PANCova estimates of evolutionary rates. Group size has been evolving slowly in nocturnal and diurnal-arboreal species (g_{NA} and $g_{DA} = 0.2$), and substantially more quickly in diurnal-terrestrial primates ($g_{DT} = 4.4$; Table 1). Despite some uncertainty (ranges for the contrasts include 0), these differences in evolutionary rates are credible ($pp < 0.1$), especially between the nocturnal and diurnal-terrestrial primates ($pp < 0.05$).

Our best fit PANCova model ($pp > 0.99$) estimated a relatively high level of phylogenetic signal for group size ($\lambda = 0.9$; Table 1). The simple Brownian motion model did not fit well ($pp < 0.01$), however, and the aistorical model also showed a poor fit ($pp = 0$). All parameters (posterior distributions available on the Online Resource: Fig. S1) were well behaved, according to all the evaluated diagnostics (Online Resource: Fig. S3 and Table S1).

Example 2. Social organization predicts trait evolution: Social complexity as a multi-state predictor

In this second example, we use social complexity as a predictor instead of a response variable, and ask whether evolutionary shifts in primate social behavior have been accompanied by changes in phenotypic evolution and diversification. Mating system and social organization have been intertwined throughout primate evolution, with a dispersed and solitary lifestyle being ancestral to primates as a whole (Verrell

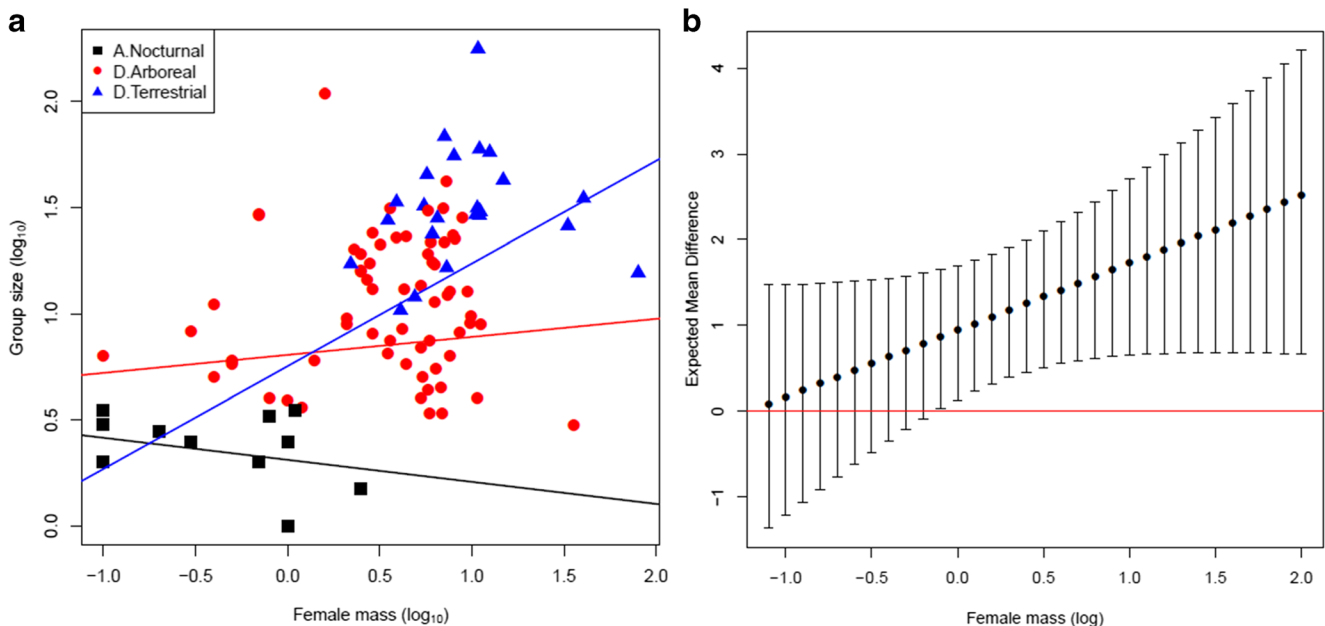


Fig. 1 **a** Relationship between group size (number of individuals/group on a log scale) and female body mass (kg, again on a log scale) for arboreal-nocturnal (black squares), diurnal-arboreal (red circles), and diurnal-terrestrial (blue triangles) primate species, with regression lines as estimated by PANCova (see Table 1 for estimates). **b** Posterior

distribution of the difference between relative group sizes for nocturnal and diurnal primates. The differences (dots) are credible (95% credible intervals excluding the red horizontal line at zero) and positive (above the red line) when female body mass > 1 kg (0 on a log scale). See text for details of data and phylogenies

Table 1 Parameter estimates from PANCOVA (Fuentes-González et al. 2016) with Bayesian extension (Fuentes-González 2018) to describe the relationship between body size and group size, and possible differences between nocturnal-arboreal (NA), diurnal-arboreal (DA), and diurnal-terrestrial (DT) species. Estimates are posterior means for all parameters except λ , for which we report the median (Steel and Kammeyer-Mueller 2008; Revell and Graham Reynolds 2012). We report also credible ranges and posterior probabilities (pp) of the estimates being larger than zero. Contrasts show pairwise differences between group effects, interactions, and phenotypic rates, with the upper diagonal showing posterior

probabilities of the parameters listed in rows being larger than those listed in columns (as such, high credibility results from posterior probabilities being very close to zero or very close to one, depending on how parameter distributions overlap; some reference credibility values available at the table footnote for comparison), and the credible ranges of the respective differences shown in the lower diagonal. Intercept estimates are labeled b_I , slopes are labeled b_S , and rates are labeled with g . Note that interaction term estimates are comparisons with the nocturnal-arboreal group. See also text and Fig. 1 for additional details

	Estimate	Range	pp	Contrasts		
Nocturnal-arboreal intercept (b_{INA})	0.3	− 0.05, 0.69	0.96**	b_{IDA}	b_{IDT}	
Diurnal-arboreal group effect (b_{IDA})	0.5	0.17, 0.82	1.00**	–	0.59	
Diurnal-terrestrial group effect (b_{IDT})	0.4	− 0.13, 1.00	0.94*	− 0.42, 0.54	–	
Nocturnal-arboreal slope (b_{SNA})	− 0.1	− 0.44, 0.24	0.24	b_{SDA}	b_{SDT}	
Diurnal-arboreal interaction (b_{SDA})	0.2	− 0.23, 0.60	0.83	–	0.06*	
Diurnal-terrestrial interaction (b_{SDT})	0.6	− 0.02, 1.19	0.97**	− 0.92, 0.11	–	
Phylogenetic signal (λ)	0.9	0.81, 0.98	1.00**	g_{NA}	g_{DA}	g_{DT}
Nocturnal-arboreal rate (g_{NA})	0.2	< 0.01, 0.60	1.00**	–	0.16	0.03**
Diurnal-arboreal rate (g_{DA})	0.2	0.04, 0.56	1.00**	− 0.73, 0.47	–	0.06*
Diurnal-terrestrial rate (g_{DT})	4.4	< 0.01, 12.80	1.00**	− 13.70, 0.52	− 12.80, 0.80	–

Credibility values: **5% ($pp < 0.05$ or $pp > 0.95$); *10% ($pp < 0.1$ or $pp > 0.9$)

1992; Dixson et al. 2005; Shultz et al. 2011; Opie et al. 2012). Social mating systems appeared later with the evolutionary appearance of multi-male aggregations and became more socially stable (i.e., less promiscuous) with transitions towards pair-living and repeated shifts to and away from polygyny (Shultz et al. 2011). The strength of sexual selection (see discussion by Shuster and Wade 2003; Jones 2009; Henshaw et al. 2016) could have increased as primates moved from dispersed to multi-male and polygynous groups, which generally have higher variance in reproductive fitness in males. Sexual selection would likely decrease again with the evolution of monogamy or pair-living.

In this example, we ask whether these changes in the intensity of sexual selection were associated with shifts in phenotypic evolution. Specifically, the baculum has often been described as serving a function in courtship and mating (Eberhard 1985; Dixson et al. 2004; Brindle and Opie 2016). However, in mammals, the baculum is a highly diverse structure that has evolved independently multiple times (Schultz et al. 2016) and which likely has different functions in different taxa, including also sperm transport and inducing ovulation (e.g., Dixson 1995; Larivière and Ferguson 2002; Brindle and Opie 2016; Orr and Brennan 2016). Thus, here, we tested for evidence of changes in relative baculum length as a result of sexual selection. Previous authors have used phylogenetic comparative analyses, for example, to show that primates with longer bacula have prolonged intermission (Dixson 1987a; Dixson et al. 2004), and that baculum length is also related to mating system (Dixson 1987b; Verrell 1992).

Similarly, baculum length does not appear to be linked to female receptivity (Stockley 2002) or testes size (Ramm 2007). Brindle and Opie (2016) conducted a comprehensive analysis of primate baculum evolution, finding that ancestral primates likely had small bacula and that longer bacula may have evolved to prolong intromission and thereby facilitate reproduction in polygamous and seasonally breeding species. All of these conclusions, however, rely on the results of fitting several separate models, for example estimating transition rates in one model, and a second model to infer the relationship between testes and baculum size. Here, we use a PANCOVA analysis to infer simultaneously evolutionary changes in baculum scaling relationships in species with different social organizations, as well as the rates of evolution in those measures.

Specifically, we used PANCOVA to compare the relationship between baculum length (y) and body size (z) in primates with different types of social organization (x), simultaneously estimating the rate of phenotypic evolution in each social context. Our model serves also as an example of PANCOVA with a multi-state predictor, because we use a single x variable to consider differences across primates in four types of social organization (dispersed, multi-male, polygynous, and pair-living). Although these categories of group size and sex composition may not fully reflect important aspects of mating systems such as mating interactions and genetic parentage, data on social organization (sensu Kappeler, this issue) are much more readily available from the literature and can be useful for generating hypotheses through comparative analyses that can

then be tested more accurately when additional data are available. By applying the PANCOPA approach, in addition to testing whether relative baculum length is associated with types of social organization, we also ask whether evolutionary shifts in these types are associated with shifts in the rate of baculum evolution. As sexual selection increases or decreases, we expect phenotypes to be more or less constrained to evolve, leading to changes also in the rate of trait evolution.

Methods

We used measures of baculum length (mm) and adult body weight (g) for 67 species from Dixon et al. (2004), and like them, we apply a log transformation on the data prior to analysis. To these, we added data on group size and sex composition as compiled from the published literature by Dixon et al. (2005) and Dixon (1987b), scoring each species as dispersed, multi-male, polygynous, or pair-living. We scored orangutans as multi-male rather than dispersed, following recent discussions on this point (Shultz et al. 2011; Opie et al. 2012). Again, we obtained a set of 1000 phylogenies from the *10kTrees* project (Arnold et al. 2010) and used stochastic character mapping (Nielsen 2002; Huelsenbeck et al. 2003) to generate a set of plausible ancestral reconstructions on type of social organization. This time, we used SIMMAP Version 1.5 (Bollback 2006), a user-friendly software with interesting properties (some of which we will briefly mention below), albeit its restricted availability (it is only available for Mac OS X). SIMMAP also uses the M_k model for standard characters (Lewis 2001), but it does so in such a way that the transition matrix (Q) can be sampled from its posterior distribution, and the root state can be sampled using conditional likelihoods and stochastic simulations from the posterior distribution of states. In this way, the user is allowed to specify prior distributions for transition rates, without requiring prior specifications for the root state. For the historical reconstruction of social organization, we generated 10 stochastic maps per tree using an empirical prior on the bias parameter and a discrete gamma prior on the overall rate of evolution ($\alpha = 10.77$, $\beta = 0.39$, $k = 60$). These priors were configured under a Bayesian procedure (Schultz and Churchill 1999) using R scripts made available by Bollback (2006) relying on the packages MASS (Venables and Ripley 2002) and TeachingDemos (Snow 2016). The resulting 10,000 reconstructions were sampled without replacement to generate an empirical prior with 1000 mappings of equal probability.

As above, we then used these data, phylogenies, and ancestral reconstructions to fit a PANCOPA model sampled under three chains of 570,000 generations total, using the first 57,000 as burn-in. Other conditions and diagnostics of the MCMC, as well as prior specifications, implementation, and inferential approaches, are as presented for Example 1.

Data availability

The datasets analyzed during the current study are included in the original contributions (see respective citations in “Methods”), and, for convenience, the merged files are available from the corresponding author on reasonable request.

Results

Using PANCOPA, we found that pair-living primates (especially marmosets and tamarins) tended to have shorter relative bacula ($0.3 \text{ mm/g body mass} = \exp.(-1.2)$, adding $b_{\text{IPL}} = -2.7$ to $b_{\text{ID}} = 1.5$ since interactions are calculated as contrasts from the dispersed group, and taking the exponent to translate from the ln scale) (Fig. 2a, Table 2). Males of species with other social systems had relatively longer bacula, ranging from 3.3–3.7 mm/g body mass for those in multi-male or polygynous groups to 4.5 mm/g body mass for males from dispersed species (Fig. 2a; Table 2). Overall, the relative size of the baculum was longer for males of species with dispersed social systems than for males of species with other types of social organization, such that the expected mean differences (i.e., the contrast or difference between mean baculum length for non-dispersed and dispersed primate species) were clearly negative for nearly all body weights (Fig. 2b). The exception to this was in the very largest-bodied species (far right of Fig. 2b) where the complete lack of dispersed primate species led to very large credible ranges.

Baculum length was related to body size in species with all four types of social organization, albeit weakly in multi-male and polygynous species (Fig. 2a, Table 2). For dispersed ($b_{\text{SD}} = 0.2$, range = 0.04, 0.35) and pair-living species ($b_{\text{SPL}} + b_{\text{SD}} = 0.4$, range = 0.05, 0.73), the slopes estimating this relationship were clearly positive, indicating a relationship between baculum length and body weight. For pair-living primates, this relationship appears to be driven primarily by a contrast between the small tamarins and marmosets and three medium-sized pair-living lemurs and gibbons (Fig. 2). Posterior probabilities for dispersed and pair-living taxa suggest further that baculum length was not independent of ($pp < 0$, for dispersed = 0.02; for pair-living = 0.01) or isometrically related to ($pp > 1$, for dispersed < 0.001; for pair-living = 0.001) body size, thus constituting clear examples of negative allometry (i.e., slope estimates falling between 0 and 1). The relationship between baculum length and body size was weakly positive for multi-male ($b_{\text{SMM}} + b_{\text{SD}} = 0.1$, range = -0.02, 0.29) and polygynous species ($b_{\text{SP}} + b_{\text{SD}} = 0.1$, range = -0.16, 0.38). Thus, it is possible that there is no relationship between baculum length and body size in these two types of social organization, especially for polygynous species ($pp < 0$, for multi-male = 0.05; for polygyny = 0.21). Credibility for an isometric relationship in the latter two

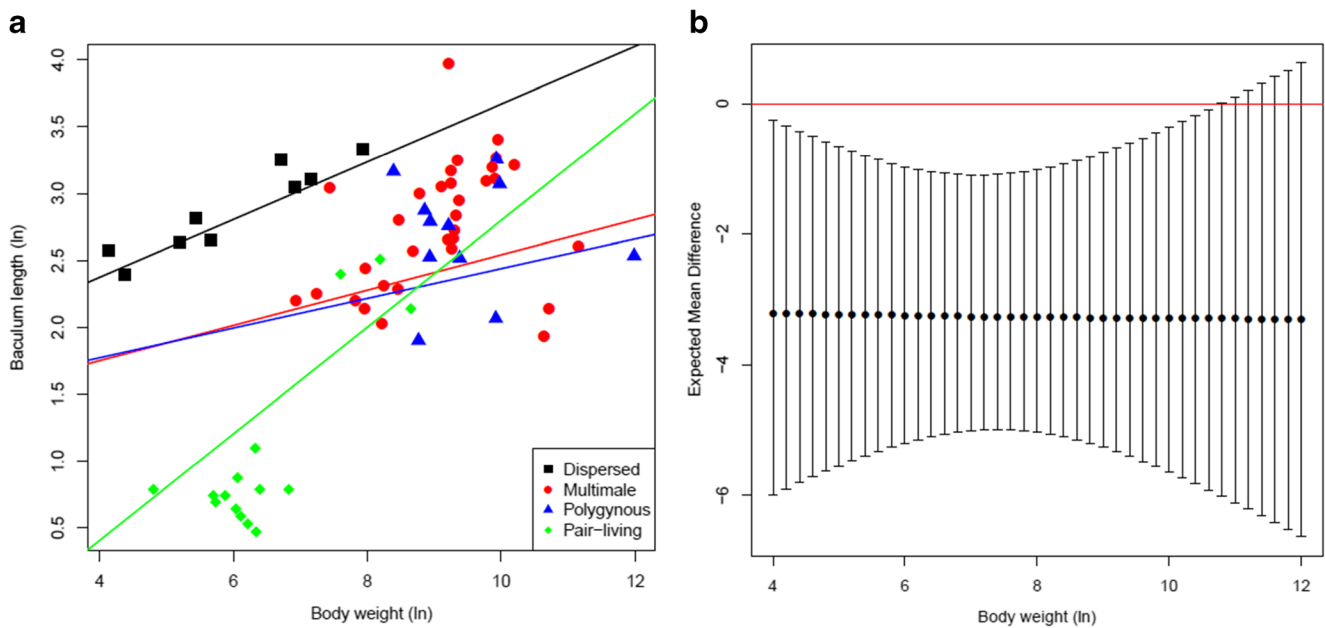


Fig. 2 **a** Relationship between baculum length (originally reported in mm) and body weight (originally reported in g) for dispersed (black squares), multi-male (red circles), polygynous (blue triangles), and pair-living (green diamonds) primate species, with regression lines as reported from PANCOVA. **b** Posterior distribution of the difference in relative baculum length between males of solitary (dispersed) and males of

more social organizations (multi-male, polygyny, pair-living). The differences (dots) are credible (95% credible intervals excluding the red horizontal line representing zero) and negative (below the red line) for body weights < 60 kg (11 on a ln scale). See text for details on data and phylogenies

systems was very low ($pp > 1$, for multi-male < 0.001; for polygyny < 0.001).

Baculum length evolved most slowly in dispersed primate species ($g_D = 0.1$), with baculum length of pair-living ($g_{PL} = 0.4$), multi-male ($g_M = 0.5$), and polygynous ($g_P = 0.6$) species all evolving more quickly (Table 2). This difference between dispersed and other types of social organization was not

particularly strong (ranges for the contrasts include 0, and $pp > 0.05$), but we confirmed the finding by computing the posterior probability that each social structure has the largest or the smallest of all rates. We found that only dispersed species had a rate of phenotypic evolution that was not credibly the largest (dispersed = 0.02, multi-male = 0.44, polygyny = 0.37, pair-living = 0.18) and that the other types of social

Table 2 Parameter estimates from using PANCOVA (Fuentes-González et al. 2016) with Bayesian extension (Fuentes-González 2018) to describe the relationship between body size and baculum length, with possible differences between dispersed (D), multi-male

(M), polygynous (P), and pair-living (PL) species. Note that interaction term estimates are comparisons with the dispersed group. Other details as in Table 1. See also text and Fig. 2 for additional details

	Estimate	Range	<i>pp</i>	Contrasts			
Dispersed intercept (b_{ID})	1.5	0.60, 2.61	1.00**	b_{IM}	b_{IP}	b_{IPL}	
Multimale group effect (b_{IM})	-0.3	-1.90, 1.34	0.36	—	0.46	0.96**	
Polygyny group effect (b_{IP})	-0.2	-3.00, 2.58	0.45	-2.75, 2.57	—	0.93*	
Pair-living group effect (b_{IPL})	-2.7	-5.28, -0.10	0.02**	-0.26, 4.96	-0.92, 5.89	—	
Dispersed slope (b_{SD})	0.2	0.04, 0.35	0.98**	b_{SM}	b_{SP}	b_{SPL}	
Multimale interaction (b_{SM})	-0.1	-0.30, 0.13	0.20	—	0.56	0.07*	
Polygyny interaction (b_{SP})	-0.1	-0.41, 0.21	0.24	-0.26, 0.29	—	0.08*	
Pair-living interaction (b_{SPL})	0.2	-0.16, 0.53	0.86	-0.61, 0.08	-0.69, 0.11	—	
Phylogenetic signal (λ)	0.9	0.65, 1.00	1.00**	g_D	g_M	g_P	g_{PL}
Dispersed rate (g_D)	0.1	< 0.01, 0.30	1.00**	—	0.06*	0.09*	0.12
Multimale rate (g_M)	0.5	< 0.01, 1.18	1.00**	-1.17, 0.12	—	0.55	0.66
Polygyny rate (g_P)	0.6	< 0.01, 1.46	1**	-1.69, 0.34	-1.29, 1.11	—	0.62
Pair-living rate (g_{PL})	0.4	< 0.01, 0.92	1**	-1.1, 0.41	-0.81, 1.11	-0.85, 1.38	—

Credibility values: **5% ($pp < 0.05$ or $pp > 0.95$); *10% ($pp < 0.1$ or $pp > 0.9$)

organization (especially multi-male and polygyny) did not credibly have the smallest rate of baculum length evolution (dispersed = 0.8, multi-male = 0.04, polygyny = 0.06, pair-living = 0.1). In other words, baculum length of dispersed species has been evolving at low to intermediate rates, whereas all of the other types of social organizations have been evolving at intermediate to high rates (although pair-living to a lesser degree).

Again, we found that incorporating phylogenetic information was important, despite considerable uncertainty in the topologies and branch lengths. In statistical terms, the probability of the model that disregards phylogenetic relationships was again negligible ($pp = 0$), and a simple Brownian motion model of phenotypic evolution also fits quite poorly ($pp = 0.12$). **PANCOVA estimated the phylogenetic signal as being quite large ($\lambda = 0.9$; Table 2)**, giving considerable weight to the respective model ($pp = 0.88$). All parameters (posterior distributions available on the Online Resource: Fig. S2) were also well behaved, according to all the evaluated diagnostics (Online Resource: Fig. S4 and Table S2).

Discussion

In Example 1, our results confirm Nunn and Barton's (2001) suspicion that habitat and activity time are important predictors of the evolutionary relationship between group and body size. As expected, we also found that shifts towards diurnal activity patterns were linked to larger relative group sizes, confirming findings that social living may have evolved with the increased predation risk of a diurnal lifestyle (Ganzhorn et al. 1985; Shultz et al. 2011). Our PANCOVA analyses go beyond earlier studies in two important ways. First, we combine continuous and multi-state categorical variables into a single analysis, following Nunn and Barton (2001) in asking about evolutionary shifts in body size, group size, habitat (arboreal/terrestrial), and activity (diurnal/nocturnal), but building a single comprehensive analysis that asks these questions simultaneously. Second, we used PANCOVA to infer the impact of our multi-state habitat-activity measure on rates of group size evolution as well as body-size scaling relationships, again simultaneously. By combining these analyses, we can ask more detailed questions about the underlying evolutionary process. Our results further focus attention on the evolution of a terrestrial lifestyle as being the critical step to forging the relationship between group and body size, and add the novel insight that diurnal-terrestrial primates not only have larger body sizes and live in larger groups, but are also undergoing more rapid group-size evolution.

In Example 2, our results suggest that as primate social organizations evolved from dispersed to more social (multi-male and polygynous), bacula became shorter, more variable in length and less subject to allometric constraints from body

size. One interpretation of this result is that the main evolutionary pattern is one of increased social stability (Shultz et al. 2011) leading to a relaxation of selection on baculum length. In dispersed species, males occupy separate home ranges, have low tolerance towards each other, and can follow an estrous female without following any sort of social structure (Dixon 1987b; Dixon and Anderson 2004). For this type of social organization, longer genitalia can be advantageous by facilitating prolonged intromission, sperm flow, and transfer of semen into the cervical canal, ultimately influencing female remating behavior and reproductive physiology while preventing penile damage (Stockley 2002; Ramm 2007; Brindle and Opie 2016). These advantages should be less prevalent in other types of organization, where social structure facilitates remating behavior regardless of genital length (Dixon 1987b; Verrell 1992). This relaxation of selection could lead to bacula that are shorter and more variable in length. Alternatively, sexual selection may have increased as primates moved to multi-male and polygynous organizations where a few males can monopolize matings (e.g., Shuster and Wade 2003). In this case, bacula may have become more variable in length because they serve different functions in different species (Schultz et al. 2016). That we did not find a difference between results for multi-male and polygynous groups is surprising, but perhaps due to primates having shifted repeatedly between these two social structures through evolutionary time (Shultz et al. 2011; Opie et al. 2012).

Both of the above interpretations are consistent with the primate fossil record that, albeit scarce, implies that ancestral primates possessed remarkably long bacula (von Koenigswald 1979; Dixon 2013). However, our results contrast with those of Brindle and Opie (2016) who concluded that since ancestral primates evolved slowly, they likely had shorter bacula comparable to those currently found in tarsiers and platyrrhines. Our PANCOVA results agree that baculum length evolved slowly in ancestral primates, but our combined analysis concludes that ancestral primate bacula were likely long, evolving to become shorter in size and more variable in length as primate species became more social. The evolutionary decrease in baculum length is further supported by our results for pair-living primates. Specifically, we found that the evolution of pair-living has been accompanied by slower evolution of the baculum, an even greater decrease in length and a return of allometric constraints. These constraints may be linked to evolutionary specialization, as pair-living is unlikely to transition back to other social structures (Shultz et al. 2011; Opie et al. 2012). But overall, our results on pair-living provide additional support for the idea that evolution of strong bonds and increased social stability has been accompanied by relaxed sexual selection on baculum length. Selective pressures such as cryptic female choice and sperm competition should be stronger in species where females mate with multiple partners, and it is in these taxa where longer bacula are

expected (Eberhard 1985; Stockley 2002; Dixson and Anderson 2004; Orr and Brennan 2016). Other analyses indicate that this could be also the case for testes mass and penile complexity (Harcourt et al. 1981; Dixson 1987b; Verrell 1992), and although the presence of such attributes could open room for trade-offs with weaponry investment (e.g., Fitzpatrick et al. 2012), the possibility seems unlikely considering that pronounced sexual dimorphism in body and canine size exist at least for multi-male and polygynous primates (Dixson et al. 2005).

Looking at our two above examples, one of the main points we would like to make is that phylogenetic comparative methods offer powerful insights into evolutionary history, despite the many limitations of crude data and incomplete phylogenies. Although group size and categories of social organization are very rough proxies of social complexity (Shultz and Dunbar 2010; Shultz et al. 2011), we used them effectively in the above examples to explore complex hypotheses about the evolution of primate social behavior in a rich and nuanced way. Similarly, despite not knowing which of several hundred phylogenies are correct, we found that historical effects were relevant for describing the data in both examples, thus confirming the importance of incorporating phylogenetic information in order to draw accurate conclusions.

We used PANCova here to illustrate the depths of interpretation possible from applying a modern phylogenetic comparative method that relies on a regression approach but incorporates both continuous and categorical measures. The mixture of continuous and categorical variables within a regression framework has been widely used for a long time, including implementations based on Monte Carlo simulations (e.g., Garland et al. 1993; Hutcheon et al. 2002) and phylogenetic generalized least squares (e.g., Butler et al. 2000; Lavin et al. 2008; West and Capellini 2016). To the well-known mean structure of these regression approaches, PANCova adds the possibility of asking questions about phenotypic diversification by relaxing the common assumption of equal phenotypic variances. As we showed in our worked examples, a comprehensive PANCova analysis can highlight interactions among different phenotypic measures and offer novel insights into the underlying evolutionary process.

There are many other methods that can offer additional insights. For example, Hansen's (1997) adaptation-inertia model explicitly models phenotypes evolving in complex selective regimes and asks how much the lack of change (stasis) can tell us about the relative importance of one or more selective factors (Hansen et al. 2008; Bartoszek et al. 2012). The use of this model has considerable interpretative advantages as it provides a microevolutionary framework that allows discussing patterns in terms of selective forces. For example, we presented above the differences of intercepts as indicative of the association between traits (i.e., baculum length, group size) and categorical factors (i.e., social organization, habitat-

activity). However, these estimates should not be interpreted as optimum values due to selective forces, as they could be interpreted under the adaptation-inertia method.

The estimation of unequal evolutionary rates has been also widely used for some time (e.g., O'Meara et al. 2006; Thomas et al. 2006, 2009), and there are actually Bayesian approaches that locate the regime shifts across the tree (Eastman et al. 2011; Revell et al. 2012; Baker et al. 2015) even within the regression framework (Barton and Venditti 2014). These approaches are great when there is little information on the factors associated with the shifts, or as a way to explore the data. However, when there is interest in testing a specific hypothetical regime, the Bayesian procedure outlined here can be particularly useful. In the examples presented above, specific hypothetical regimes (habitat-activity and social organization) were relevant because they informed the social complexity hypotheses, and yet, the results were not conditioned by any given regime reconstruction because the joint posterior distribution accounted for the combined sources of uncertainty (including the mappings of categorical factors). Thus, both approaches are useful but differ in the source of uncertainty incorporated in the analysis. The former places the uncertainty on shift positions of an unknown factor, while the latter places the uncertainty on the reconstruction of a known factor. The question and type of data should guide the selection of one method over the other, or even better, both approaches could be used concomitantly for a more comprehensive understanding of the pattern at hand. Other methods incorporate fossil, climate, or biogeographic information (e.g., Lawing et al. 2016), or focus on different ways to consider historic and ahistorical factors (e.g., Lynch 1991; Housworth et al. 2004; Hadfield and Nakagawa 2010).

A strong relevance of evolutionary history for explaining the pattern is not the only attribute shared by our two examples. Both stories involve the evolution of social attributes and the relaxation of constraints in other features. In the first example, larger and more variable groups possibly facilitated the transition towards more risky life-styles by reducing predation pressures (Nunn and Barton 2001; Shultz et al. 2011). In the second example, shifts in social organization released constraints on the evolution of baculum length. The initial development of the PANCova includes a third example in which the evolution of parental care in birds may have released constraints on the evolution of telencephalon size (Fuentes-González et al. 2016). In all three cases, these patterns may not have been detected in studies that focused solely on means (e.g., Butler et al. 2000; Hutcheon et al. 2002; Lavin et al. 2008; West and Capellini 2016) or variances (e.g., O'Meara et al. 2006; Thomas et al. 2006), as both elements were important in recognizing how the constraints were released. Here, we advocate for combined approaches such as the PANCova that simultaneously evaluate trait relationships

and evolutionary rates, and a careful, detailed view of the underlying evolutionary process.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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