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The role of behavioural flexibility in primate diversification

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ABSTRACT:

Understanding impacts on species diversification is fundamental to our understanding of the evolutionary processes underlying biodiversity. The 'behavioural drive hypothesis' posits that behavioural innovation, coupled with the social transmission of innovative behaviours, can increase rates of evolution and diversification, as novel behaviours expose individuals to new selection regimes. We test this hypothesis within the primates, a taxonomic group with considerable among-lineage variation in both species diversity and behavioural flexibility. We employ a time cut-off in our phylogeny to help account for biases associated with recent taxonomic reclassifications and compare three alternative measures of diversification rate that consider different phylogenetic depths. We find that the presence of behavioural innovation and social learning are positively correlated with diversification rates among primate genera, but not at shallower taxonomic depths. Given that we find stronger associations when examining older as opposed to newer diversification events even after controlling for potential sampling biases, we suggest that extinction resistance may be an important mechanism linking behavioural flexibility and diversification in primates. If true, our findings offer support for an expanded view of the behavioural drive hypothesis, and key predictions of this hypothesis can be tested as primates are forced to respond to ongoing environmental change.

KEYWORDS: behavioural drive; behavioural flexibility; evolutionary diversification; primates; speciation

Extant species diversity is remarkably variable across the Tree of Life (Willis, 1922; Williams, 1964). For clades of the same age, differences in net diversification rate (i.e. speciation rate

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minus extinction rate) ultimately drive differences in clade size. Both the external environment (e.g. Badgley, 2010; Kozak & Wiens, 2010; Frey, 2010) and intrinsic features of a lineage (e.g. Raikow, 1986; Heard & Hauser, 1995) can influence net diversification. Despite ongoing study, there remains considerable debate over the factors that lead to differences in diversification rate among lineages, and their relative importance (e.g. Lewontin, 1983; West-Eberhard, 1989; Isaac, et al., 2005; Rabosky, 2009; see review by Wiens, 2017).

Plasticity has been repeatedly proposed to play a major role in shaping evolutionary trajectories in general, and speciation in particular (Baldwin, 1902; Lewontin, 1983; Bateson, 1988; Wcislo, 1989; Odling-Smee, et al., 2003; West-Eberhard, 2003; Pelletier, et al., 2009), and theoretical modelling supports its potential influence (e.g. Hinton & Nowlan, 1987; Anderson, 1995; Behera & Nanjundiah, 1995; Ancel, 1999; 2000). Behavioural development and expression often allow for more rapid responses than other forms of plasticity such as induced morphological changes (Duckworth, 2009; Snell-Rood, 2013; West-Eberhard, 2003). Thus, behaviour in particular has been hypothesized to influence evolutionary rates, particularly lineage diversification (Wyles, et al., 1983; Wilson, 1985; West-Eberhard, 2003). Notably, the ‘behavioural drive hypothesis’ posits that behavioural innovation, coupled with social transmission, increases rates of evolutionary diversification as populations that adopt novel behaviours are exposed to new selective regimes and eventually diverge from their ancestral lineage (Wyles, et al., 1983; Wilson, 1985). Thus, behaviourally flexible taxa (i.e. those taxa exhibiting high propensities for behavioural change due to, for example, learning or readiness to transition to new conditions (Sol & Lefebvre, 2000; Audet & Lefebvre, 2017)) are predicted to show faster rates of evolutionary change, and eventual evolutionary diversification, compared to less flexible taxa (Sol, et al.,

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2005). However, despite theoretical support (e.g. Price, et al., 2003; Lachlan & Servedio, 2004; Lapiedra, et al., 2013), the behavioural drive hypothesis remains contested. Some dispute the extent to which behaviour plays any active role in animal evolution (e.g. Scott-Phillips, et al., 2014) while others suggest that behavioural flexibility is more likely to inhibit than enhance species diversification: populations that can utilize new resources or transition to new environments are shielding their genomes from bouts of strong directional selection, a hypothesis termed 'behavioural inhibition' (Huey, et al., 2003; Duckworth, 2009). These conflicting views make it clear that relationships between behavioural flexibility and diversification across taxa have yet to be fully elucidated.

In this context of opposing views, Duckworth (2009) suggests that behavioural drive and behavioural inhibition can both play a role in shaping evolutionary processes. Under this proposed framework behavioural inhibition acts on short time scales to buffer abrupt environmental changes that may otherwise result in a population bottleneck or strong bouts of directional selection. Over longer timescales, the same behavioural shift can also initiate behavioural drive, either by setting the stage for allopatric speciation or by exposing the newly situated population to novel selection regimes (Huey, et al., 2003; Losos, et al., 2004; Duckworth, 2009; see example in Muñoz & Losos, 2018).

Previous studies have provided support for both behavioural drive (e.g. Yeh, 2004; Yeh & Price, 2004; Tebbich, et al., 2010, Riesch, et al., 2012; Foote, et al., 2016) and behavioural inhibition (e.g. Losos, et al., 2004; Weber, et al., 2004; Shultz, et al., 2005; Gonzalez-Voyer, et al., 2016).

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However, many of these studies have primarily considered the effects of behavioural flexibility on micro-evolutionary change at short time scales (e.g. recent speciation events or population decline). Three comparative studies have tested for the macro-evolutionary effects of behavioural flexibility on lineage diversification across multiple lineages, all in birds (Nicolakakis, et al., 2003; Sol, et al., 2005 – also see Sol, 2003; Sayol, et al., 2019). These studies have employed two proposed correlates of behavioural flexibility: brain size relative to body size (a structural measure presumed and shown elsewhere to be associated with behavioural flexibility; e.g. Lefebvre, et al., 2004) and innovation rate (a behavioural measure) taken from literature surveys. Both large relative brain size and high innovation rates were associated with heightened diversification in birds (Nicolakakis, et al., 2003; Sol, et al., 2005; Sayol, et al., 2019), consistent with the behavioural drive hypothesis. However, such tests have yet to be applied across other taxa, making it difficult to generalize the role of behaviour in shaping the Tree of Life.

Here, we explore the relationship between four proxies of behavioural flexibility and several measures of diversification rate (see Methods) in the Primates, a taxonomic group with considerable among-lineage variation in several measures of behavioural flexibility (Reader & Laland, 2002; Reader, et al., 2011) and extant species diversity (Upham, et al., 2019a; 2019b). Variables associated with diversity of other taxa (e.g. geographic range size and latitude) have been shown to be poor predictors of primate diversification (Arbour & Santana, 2017; Upham, et al., 2019a), leaving a great deal of what shapes extant primate diversity unexplained. We focus on two behavioural measures of behavioural flexibility, the presence or absence of published reports of innovation and of social learning, and two brain size measures widely thought to be associated with ability to exhibit flexible behaviours. We predict that our separate measures of

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behavioural flexibility will covary positively with diversification rates across primate lineages. To examine how this association changes at different evolutionary timescales, we examine how behavioural flexibility correlates with diversification over both shallow and deeper time depths in our phylogeny. Understanding how behaviour and ecology may interact to shape evolutionary patterns provides a glimpse into some of the processes that have shaped the past, and may in turn dictate the future biological diversity among primates.

METHODS:

Rationale

Innovation and social learning are both important for behavioural drive because multiple individuals must acquire an innovation by social learning or independent innovation to have population-level effects (Wyles, et al., 1983; Wilson, 1985; Duckworth, 2009). In addition to facilitating the transmission of innovations throughout a population, social learning can also be a valuable measure of population-level behavioural flexibility on its own as it reflects the ability of individuals within a population to pick up behaviours that are novel to them but not necessarily novel to the population. We note that social learning and innovation are taxonomically widespread (Reader & Biro, 2010; Snell-Rood, et al., 2015). However, we assume that species with no published accounts of social learning or innovation are likely relying on these behaviours infrequently. Moreover, the innovation and social learning data used here have been positively associated with other measures of behavioural flexibility (Reader, et al., 2011; Navarrete, et al., 2016). For innovation, we focus on technical innovations (classified as those involving tool use following Navarrete, et al., 2016) because these more easily defined behaviours have been linked

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to complex cognition (Overington, et al., 2009), and reports of other classes of innovation (e.g. food type innovation) can be highly influenced by opportunistic events (Ducatez, et al., 2015). Combined with the fact that taxa with reports of technical innovation also tended to be those with evidence of other innovation types (see data in Navarrete, et al., 2016), this likely makes technical innovation a robust estimate of innovativeness across primates.

Literature-based evidence for behavioural flexibility across taxa has its limitations and so we chose to also consider structural correlates of behavioural flexibility. It is widely thought that particular brain regions are associated with flexible behaviour – particularly the neocortex (see e.g. Keverne, et al., 1996; Mikhalevich, et al., 2017) and cerebellum (Vandervert, 2003; Vandervert, et al., 2007; Barton, 2012). Therefore, in addition to total brain size (relative to body mass), we considered the sum of neocortical and cerebellar volumes relative to rest of total brain volume as another proxy for behavioural flexibility. We note that while brains perform many functions and the link between volume and function is not well established (e.g. Healy & Rowe, 2007; Logan, et al., 2018), behavioural flexibility measures such as innovation rate, social learning rate and learning performance in the laboratory do correlate with brain volume measures across species (Reader, 2003; Lefebvre, et al., 2004; Reader, et al., 2011). This suggests that primate brain volume measures are useful secondary proxies of behavioural flexibility. While direct measures of behavioural flexibility under standardized testing conditions would be valuable, such measures are not available for the large-scale comparative tests we conduct here. We can however compare the consistency of results across different proxies for behavioural flexibility.

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Diversification rate (our dependent variable) is not straightforward to measure. In particular, the influence of taxonomic reclassifications, namely those associated with the introduction of the 'phylogenetic species concept' (PSC) can lead to biased species designations across taxa (Tattersall, 2007; Rylands & Mittermeier, 2014), particularly through the elevation of subspecies to the full species rank. Taxonomically-biased species designations will in turn bias diversification metrics such as the number of species in a taxon divided by its age. We attempt to minimize such taxonomic biases in order to produce a consistent measure of diversification rate across taxa by including a time cut-off in our phylogeny (see next section), a method that might be useful for future studies of species diversification.

Data

Diversification Rate

Estimating diversification rates is challenging because it depends on an accurate assessment of both the taxonomic richness and divergence time of a given lineage. A previous study testing the effect of behavioural drive at shallow time depths used subspecies per species as a measure of subspecific diversification (Sol, et al., 2005); in primates taxonomic richness has changed drastically over recent decades (Tattersall, 2007; Groves, 2014), with much of this change attributed to application of the 'phylogenetic species concept' (PSC) and its tendency to raise former subspecies and variants to the full species rank (Tattersall, 2007). Importantly, it has been suggested that these elevations in subspecies status have been biased toward certain taxa (Isaac, et al., 2004), which would lead to inconsistent estimates of species versus subspecies richness across lineages. Studies using other estimates of primate diversification (i.e. diversification

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analyses using TreePar; Stadler, 2011) have been hindered by the applications of the PSC, particularly when it comes to accurately estimating shallow divergences (Springer, et al., 2012). Modern primate phylogenies are also not reflective of modern primate taxonomies, including some phylogenetic species and omitting others, preventing us from using recently described evolutionary rate measures that rely on a comprehensive phylogeny with consistent species estimates among clades. Instead, we used well-resolved “lineages” that putatively reflect stable species complexes. We started with the most widely used, dated primate tree publically available at the time of this study, the GenBank taxonomy consensus tree provided on the 10kTrees website (version 3) (Arnold, et al., 2010), containing 301 tips. We then created a time cut-off in the tree at the time when we determined a majority of robust biological species described in Honacki et al. (1982) had evolved (1.1mya), subsequently eliminating shallower divergences after this time cut-off from the consensus tree (see Figure S1). Honacki et al. (1982) is the last major primate taxonomy published before the introduction of the PSC (Cracraft, 1983). Each branch in the tree that was extant 1.1mya we designated a "lineage." We also eliminated species no longer recognized by modern taxonomies (IUCN/SSC Primate Specialist Group, 2018). This resulted in 241 identifiable lineages to compare in terms of taxonomic richness and divergence times. Using the most recent published primate species and subspecies list from the IUCN/SSC Primate Specialist Group (2018), we referenced taxonomic and phylogenetic works to assign each of the 705 species and subspecies to one of these 241 lineages. This allowed us to assign an agnostic “taxon richness” score to each lineage (see Figure S1) that accounts for the discrepancies in subspecies elevations across lineages. Because higher level classifications have also been affected by taxonomic changes, each species or subspecies listed by the IUCN/SSC Primate Specialist Group (2018) was also assigned to one of the 66 genera named in our

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10kTrees phylogeny (Arnold, et al., 2010). After eliminating two species and one genus in our tree that could not be resolved using these methods (see electronic supplementary materials), our study considered 703 taxa (species or subspecies) assigned to 239 lineages and 65 genera.

To estimate lineage diversification rate, the natural log of "taxon richness" for each lineage in our tree was divided by the stem age of that lineage using the method-of-moments approach described in Magallon & Sanderson (2001) to produce a 'Taxa per Lineage Diversification Rate' that should be unbiased by recent subspecies elevations. This method was repeated at the genus level where the natural log of "taxon richness" for each genus was divided by the stem age of that genus (hereafter 'Taxa per Genus Diversification Rate'). Lastly, we created a second, and perhaps more conservative estimate of genus diversification where richness scores were generated using the number of lineages per genus, rather than the number of taxa described by the IUCN/SSC Primate Specialist Group (2018), hereafter 'Lineage per Genus Diversification Rate'. We found that there were several instances of non-monophyletic genera within the phylogeny (*Galagoides*, *Otolemur*, *Galago* and *Euoticus*). As such, we elected to retain these lineages in our lineage-level tree (as their unresolved nature may simply be due to taxonomic issues; Masters, et al., 2017), but removed these genera from genus-level analysis as it is unclear how to assign a stem age to these clades. We additionally removed the genus *Semnopithecus*, which comprised a single lineage nested within the genus *Trachypithecus*. Thus, while our lineage-level dataset contained lineages from 65 genera, our genus-level analysis considered only 60 genera. Lineages of *Cercopithecus* were also resolved as polyphyletic in the phylogeny, with a small fraction of lineages forming a clade sister to *Erythrocebus*. Since a majority of *Cercopithecus* lineages were resolved as monophyletic, we opted to assign *Cercopithecus* the

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divergence date that separates it from the clade of *Chlorocebus* and *Erythrocebus*; we note that removing *Cercopithecus* in its entirety did not qualitatively change the results we report here.

We illustrate these methods and present associated calculations using genus *Aotus* as an example in the electronic supplementary materials.

Structural Proxies of Behavioural Flexibility

Lineage-level estimates for all brain measures were calculated by taking the geometric mean of taxon volumes for each lineage. Genus-level estimates were calculated by subsequently taking the geometric mean of these lineage estimates for each genus.

Using lineage-level estimates, we regressed logarithmic endocranial volume in cm^3 (ECV) (Powell, et al., 2017) (hereafter 'brain volume') as a function of logarithmic body mass (Jones, et al., 2009) and retained the residuals (Dunbar & Schultz, 2007). These residuals (hereafter 'relative brain volume') were repeated using genus-level estimates and were used in subsequent analyses to test the association between brain volume relative to body mass and diversification rate at both the lineage and genus-level (Lefebvre, et al., 1997; Sol, et al., 2005). Residual analyses may lead to an inflation of type II error as it is a very conservative method of controlling for body size (Darlington & Smulders, 2001), however, including both variables in a multiple regression as suggested by some (e.g. Freckleton, 2002) caused brain volume and body mass to compete within our models (results not shown), seemingly inflating resulting effect sizes. As a result, we chose to use the more conservative approach based on residual brain volume.

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Data for neocortex, cerebellum and rest-of-brain volume were obtained from Navarrete et al. (2018) and the compilation in DeCasien & Highman (2019). The DeCasien & Highman (2019) compilation includes data from the prior Reader & Macdonald (2003) compilation and contains brain component volumes from multiple studies, largely Stephan et al. 1970, 1981, and 1988 (see electronic supplementary materials). Absolute neocortex and cerebellum volumes covary with total brain volume and so we again used lineage-level brain estimates and took residuals from a log-log regression of the combined neocortex and cerebellum volumes on the rest-of-brain volumes (i.e. total brain volume minus neocortex and cerebellum volumes). These residuals (hereafter 'relative neocortex and cerebellum volume') were repeated using genus-level brain estimates and used to test the relationship between neocortex and cerebellum volume and diversification rate at both the lineage and genus-level.

Behavioural Proxies of Behavioural Flexibility

Counts of innovation and social learning per lineage came from Reader et al. (2011) and Navarrete et al. (2016). Reader et al. (2011) established this dataset through a survey of over 4000 published articles for examples of social learning and behavioural innovation. Reader et al. (2011, p. 1018) define an innovation as the tendency to "discover novel solutions to environmental or social problems". These data were later subdivided into different innovation categories by Navarrete et al. (2016), including 'technical' innovations, defined as innovations involving tool use. Reader et al. (2011, p. 1018) define social learning as the tendency to "learn skills and acquire information from others", including instances of social learning from both kin

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and unrelated individuals. Social learning was often inferred from observational data in the original reports. Experimental data would be preferred (Reader & Biro, 2010) but are not available for the wide taxonomic spread of our study. The innovation and social learning counts provide quantitative comparative data for a large number of species, typically from observations in the wild. Despite acknowledged weaknesses of such observational data (discussed in Lefebvre, et al., 1997; Laland & Reader, 1999; Reader, 2003; Reader & MacDonald, 2003; Reader, et al., 2011), the taxonomic spread allows for tests of large-scale macro-evolutionary trends that can then be followed up by targeted experimental approaches.

As an alternative to treating behavioural data as a binary metric (e.g. innovativeness in Ducatez, et al., 2020), other studies have used "rate" measures of behaviours: residuals from a log-log plot of the total number of recorded instances of a behaviour (e.g. social learning) and an estimate of research effort (e.g. the number of papers published on that taxa; e.g. Sol, et al., 2005; Reader, et al., 2011; Navarrete, et al., 2016; Ducatez, et al., 2020). However, we opted to use binary measures, allowing us to use data imputation methods to minimize any biases caused by under-studied taxa, to statistically account for potential biases associated with summarizing behavioural data at higher taxonomic levels, and to run simulations to address the assumptions underlying our analyses. We therefore assigned each lineage or genus binary scores of 1 (presence of innovation or social learning) or 0 (absence of innovation or social learning). As a test, we fit a log-log Model I regression of both technical innovation and social learning on research effort as reported for species by Reader et al. (2011) and retained the residuals, and plotted these residuals against the presence (1) and absence (0) of these behaviours; as expected, the binary measure captured rate measures well (Figures S2 and S3). Correlation coefficients for predictor variables

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can be found in the electronic supplementary material (Table S1) along with reports of phylogenetic patterns observed among predictor and response variables (Table S2).

Genus-level Simulations

We scored each lineage as exhibiting technical innovation or social learning if there was any positive evidence for such a behaviour across the tips, thus assuming the behaviour was ancestrally present in the lineage rather than derived only in the taxon or taxa where it was observed. However, scoring genera as exhibiting flexible behaviour if recorded in any of its lineages could lead to a statistical bias if more lineage-rich genera (which will generally have higher diversification rates) are more likely by chance to include at least one lineage that expresses technical innovation or social learning. Fortunately, it is straightforward to simulate the evolution of these traits on our tree independently of diversification rate to quantify this sampling effect, and to ask if any observed correlations depart from this expectation. We simulated the evolution of lineage-specific technical innovation and social learning on the phylogeny over 500 iterations using the symmetrical rate Mk model of discrete trait evolution (Lewis, 2001; Harmon, et al., 2008), parameterized with the observed transition rates from our lineage dataset. We included imputed data for estimating transition rates, noting that removal of these points did not meaningfully influence transition rates. After simulating the evolution of these traits 500 times, we repeated genus-level analyses over the resulting datasets. We present results from the relevant null model simulations in the electronic supplementary materials and report the probabilities of obtaining the observed effect sizes by chance (the proportion of null-generated effect sizes that exceeded the observed effect size in these 500 simulations) to test whether our observed effect sizes could be explained by this potential sampling bias.

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Analysis

Trait Imputation

While we collected data for brain size, body mass, and behavioural flexibility from the most comprehensive datasets and compilations available, research biases and the persistent reassessment of primate taxonomy has resulted in inconsistent data coverage across lineages, and there were still many lineages that were missing data (see Figure S4). To maximize our evolutionary inferences on diversification and allow for the inclusion of data-poor lineages, we chose to impute missing predictor variables using phylogenetic imputation methods (see electronic supplementary materials for details and reports of predictive accuracy from model cross-validation; Table S3). Data on relative neocortex and cerebellum volume were sparse and unevenly distributed across the phylogeny (82.4% of lineages missing data; Table S3), making it infeasible to reliably impute missing values. We thus only ran models of relative neocortex and cerebellum volume on the original, non-imputed dataset. All of the regressions we report below were repeated for the original, non-imputed datasets (see Results and the electronic supplementary material Tables S4, S5 and S6) and except as noted below gave a similar pattern of results.

Predictors of diversification

To assess the relationship between our measures of behavioural flexibility and diversification rate at the lineage-level (Taxa per Lineage Diversification Rate) we used phylogenetic generalized least squares (PGLS) regressions with the 10kTrees consensus tree including our 239

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defined lineages. PGLS is a common regression method used to investigate evolutionary associations while accounting for the fact that closely-related lineages tend to be similar (e.g. in body size, life history and ecology; see Freckleton & Harvey, 2002). Continuous data (relative brain volume and relative neocortex and cerebellum volume) were $\log_e$-transformed and scaled by 2 standard deviations in all models for both the lineage and genus-level analyses (Gelman, 2008). After imputing missing values, our dataset contained 52 lineages scored as having evidence of social learning (scored as 1) and 28 lineages scored as having evidence of technical innovation (scored as 1). Wyles et al. (1983) predicted accelerated evolution in species with a dual capacity for innovation and social propagation of new behaviours, therefore, we also tested a combined measure of technical innovation and social learning. In this combined measure lineages with the presence of both behaviours were scored as 1 (n=25), and those exhibiting only one or neither behaviour were scored as 0 (n=214).

To assess the relationship between our measures of behavioural flexibility and diversification rate deeper in the tree we repeated the same analysis at the genus-level using two different estimates of diversification rate: Taxa per Genus Diversification Rate and Lineage per Genus Diversification Rate. Lineage per Genus Diversification Rate could be considered a conservative estimate that omits shallower divergences. After imputing missing values, our dataset of 60 genera contained 21 genera scored as having evidence of social learning, 9 genera scored as having evidence of technical innovation and 8 genera with evidence of both behaviours.

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Body mass and attendant life history traits have been predicted to impact diversification rates in some taxa with conflicting results (e.g. Cardillo, et al., 2003; Paradis, 2005; Fontanillas, et al., 2007; Thomas, et al., 2010), and body mass is closely correlated with many primate life history traits (e.g. age at first reproduction, maximum lifespan; Charnov & Berrigan, 1993; Purvis, et al., 2003; Street, et al., 2017). To examine further whether our results could stem from confounding effects of body mass and its correlates, we ran PGLS analyses to test body mass as an independent predictor of our diversification rate measures. Results from these tests were non-significant across all measures of diversification (see electronic supplementary material Tables S4 to S6). All analyses used R version 3.6.3 (R Core Team, 2020).

RESULTS:

Lineage-level predictors of diversification

We found either weak or no support for the behavioural drive hypothesis when testing our measures of behavioural flexibility at the lineage level (results summarized in Figures 1 and S6; Table S4). Social learning had the strongest association with Taxa per Lineage Diversification Rate, whereby primate lineages exhibiting social learning had faster mean diversification rates (0.319 species my^{-1}) than non-social learning lineages, but this did not reach statistical significance (0.228 species my¯1; ß [95% CI] =0.091 [-0.006-0.188]; p= 0.066). Technical innovation (p= 0.792), the combined presence of technical innovation and social learning (p= 0.741), relative brain volume (p= 0.215), relative neocortex and cerebellum volume (p= 0.664), and body mass (p= 0.764; Table S4) did not exhibit noteworthy associations with Taxa per Lineage Diversification Rate in either direction.

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Genus-level predictors of diversification

Technical innovation (p= 0.577), social learning (p= 0.442), the combined presence of technical innovation and social learning (p= 0.411), relative brain volume (p= 0.058), relative neocortex and cerebellum volume (p= 0.987), and body mass (p= 0.204) did not exhibit noteworthy associations with Taxa per Genus Diversification Rate (Figures 1 and S6; Table S5). Patterns were similar using the non-imputed dataset (Table S5), though there was a significant positive relation between relative brain volume and Taxa per Genus Diversification Rate (p= 0.004). Although the non-imputed data may suffer from sampling biases, it shows similar patterns overall, and the relationship between relative brain volume and Taxa per Genus Diversification Rate becomes much stronger.

In contrast to the other diversification measures, Lineage per Genus Diversification Rate was positively associated with all three behavioural measures of behavioural flexibility (results summarized in Figures 1 and S6; Table S6). Genera with records of technical innovation were shown to have a faster mean Lineage per Genus Diversification Rate (0.136 lineages my^{-1}) than those with no reports (0.070 lineages my^{-1}; ß [95% CI] =0.066 [0.002-0.130]; p= 0.048). Genera with records of social learning similarly exhibited a faster mean Lineage per Genus Diversification Rate (0.137 lineages my^{-1}) than those which had no reports of social learning (0.049 lineages my^{-1}; ß [95% CI] =0.088 [0.043-0.132]; p< 0.001). Finally, genera with reports of both technical innovation and social learning exhibited a faster mean Lineage per Genus Diversification Rate (0.153 lineages my^{-1}) compared to those with evidence for only one or

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neither behaviour (0.068 lineages my^{-1}; ß [95% CI] =0.085 [0.018-0.151]; p= 0.015). However, relative brain volume (p= 0.253), relative neocortex and cerebellum volume (p= 0.684) and body mass (p= 0.268) did not share notable associations with Lineage per Genus Diversification Rate (Figures 1 and S6; Table S6).

Genus-level Simulations

These observed positive correlations between our measures of behavioural flexibility and genus-level estimates of diversification rate could arise from chance: with more lineages there is a higher probability that a propensity to innovate or to socially learn may arise and be subsequently conferred to the entire genus. To account for this, we simulated the random evolution of the presence of social learning and technical innovation across the primate phylogeny using a symmetrical Mk model and observed transition rates. We found that indeed there is a bias towards a positive relationship between diversification rate and the presence of each behavioural flexibility measure (supplementary Figures S7 to S9); however, our results for Taxa per Genus Diversification Rate remained non-significant and for Lineage per Genus Diversification Rate remained significant after adjusting for our expected effect sizes. For Taxa per Genus Diversification Rate, the probabilities of the observed effect sizes (ß) occurring by chance were p=0.392 for presence of technical innovation, p=0.420 for presence of social learning, and p=0.260 for combined presence of technical innovation and social learning. For Lineage per Genus Diversification Rate, the probabilities of the observed effect sizes (ß) occurring by chance were p=0.028 for presence of technical innovation, p=0.002 for presence of social learning, and p=0.008 for combined presence of technical innovation and social learning.

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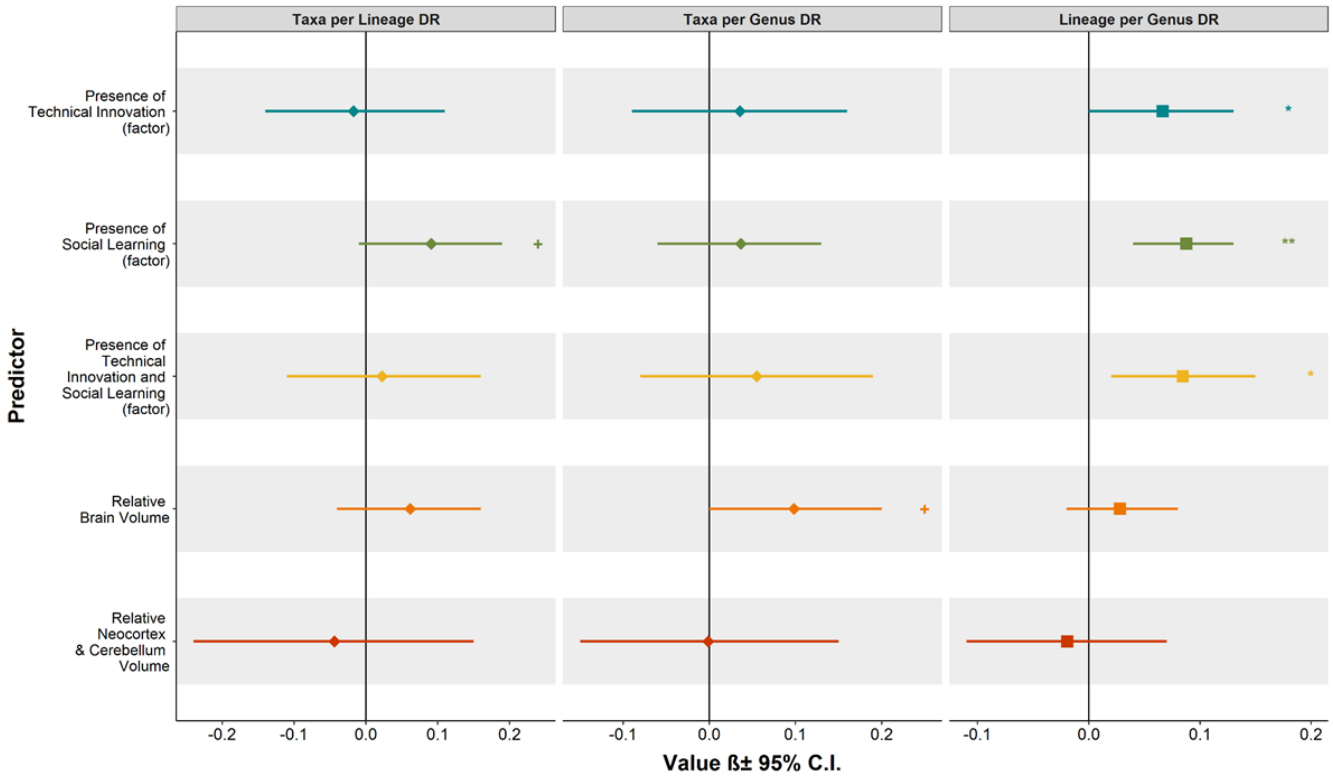

Figure 1: Results from PGLS analyses showing the association of proxies of behavioural flexibility with Taxa per Lineage Diversification Rate (DR), Taxa per Genus Diversification Rate and Lineage per Genus Diversification Rate across primates. 95% confidence intervals are represented by horizontal lines around the associated value. Diamonds indicate diversification rates estimated with species/subspecies richness, and squares indicate diversification rates estimated with lineage richness. Results presented include imputed data when available and brain measures were standardized (ln x/(2sd)). Significance indicated as: +P≤0.1; * P<0.05; ** P<0.01.

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DISCUSSION:

We examined how behavioural flexibility correlates with primate diversification over both shallow and deeper time depths in our phylogeny using three diversification measures. We find little to no compelling support for an association between our proxy measures of behavioural flexibility and diversification at shallow depths, but do find evidence for a positive association when looking at older primate lineages: Lineage per Genus Diversification Rate was on average higher in taxa with reports of innovation, social learning, and innovation and social learning together compared to other taxa. This pattern could suggest a nuanced effect of behaviour on diversification that differs from the original formulation of the behavioural drive hypothesis.

One benefit of our study design is that it allowed us to consider taxa that are commonly overlooked (i.e. subspecies and species omitted from higher-order phylogenies), many of which likely represent shallow splitting events. The weak associations with behavioural flexibility that we observed at shallower time-scales could be explained in several ways. On one hand, this pattern could be reflective of biases in describing taxa (species and subspecies) among groups. While our time cut-off and our use of both species and subspecies mitigates against biases associated with the elevation of subspecies under the PSC, if less flexible species are more likely to have a larger number of taxa described overall, this could obscure underlying biological patterns. In this case, the lineages per genus results are less biased. If this is the case, then behavioural flexibility may enhance diversification overall as proposed by Wilson et al. (Wyles, et al., 1983; Wilson, 1985), and we observe stronger associations when ignoring shallow splits. On the other hand, if we take our results at face value, the pattern of stronger associations at

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deeper levels could indicate that time plays an even larger role in the relationship between behavioural flexibility and diversification than previously suggested by Duckworth (2009).

Under Mayr's 'ephemeral speciation model' (Mayr, 1963; Rosenblum, et al., 2012) and the related 'ephemeral divergence hypothesis' (Futuyma, 1979; 2010), divergence can occur rapidly and often, but many newly diversifying lineages do not persist, instead being eradicated via extinction or 'reabsorption' by hybridization (see, e.g., Rosenblum, et al., 2012). It is possible that a number of the described species and subspecies used here (IUCN/SSC Primate Specialist Group, 2018) represent such ephemeral diversification events, especially considering that the PSC has facilitated the splitting of very closely related populations. If so, our results could be explained if behavioural flexibility is buffering against extinction of recently diverged species through behavioural shifts, thereby influencing lineage persistence rather than rate of splitting, leading to a stronger relationship when comparing the accumulation of lineages deeper in the tree. This would be complementary to findings from Arbour & Santana (2017), who show that decreased extinction preceded a shift to increased evolutionary rates in the most speciose primate family (Cercopithecidae), along with evidence suggesting behavioural flexibility is beneficial for population persistence in birds (e.g. Shultz, et al., 2005; Rossmanith, et al., 2006; Sol, et al., 2007, Ducatez, et al., 2020). Whether behavioural flexibility does act to reduce extinction in primates may be revealed going forward as biodiversity loss unfolds. Under this scenario, even under the assumption that these behaviours are ancestral to genera, the positive associations we find seem unlikely to support behavioural flexibility promoting diversification as per the behavioural drive hypothesis: behavioural flexibility does not seem to be driving recent, shallow divergences in primates. This contrasts to evidence found in birds (Nicolakakis, et al., 2003; Sol,

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et al., 2005; Sayol, et al., 2019) and suggests that either there is no generalizable relationship between behaviour and lineage diversification, or that we need to focus on extinction rather than speciation to understand the macro-evolutionary effects of behavioural flexibility in primates.

One avenue to help determine why we observe stronger associations deeper in the tree would be to compare genetic variation in flexible versus inflexible lineages. We predict that if behavioural flexibility leads to faster diversification through faster rates of divergence, then unsupervised genetic clustering of species and subspecies gene sequences should find more distinct clusters, relative to time, in flexible versus inflexible lineages. If this is not the case, such that genetic sampling does not reveal increased divergence relative to time in flexible groups, this would provide additional support for behavioural flexibility dampening extinction.

One notable limitation of our study is that one measure thought to be associated with behavioural flexibility – neocortex and cerebellum volume – had very little data available for lineages reported as inflexible (e.g. among lemurs, tarsiers, titis and sakis), partly because we required measurements of neocortex, cerebellum and total brain volume to be for the same specimen. More data are needed to fully test these measures as drivers of diversification. Our study is also limited by lineages and relationships present in our phylogeny (Arnold, et al., 2010). Available primate phylogenies, (e.g. Arnold, et al., 2010; Upham, et al., 2019b) do not reflect the most recent taxon lists. The tips available in our phylogeny prevented us from using diversification rate estimates that require a fully-resolved tree (e.g. the DR measure from Jetz, et al., 2012) and/or that incorporate extinct lineages (e.g. Mitchell & Rabosky, 2017). However, we suggest that our method for measuring diversification rate could be applied more broadly across studies

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of species diversification as it presents a solution to the common problem of species definitions, allows for the consideration of recent splitting events, and can be applied in taxa where available phylogenies lack the appropriate tree tips for alternative diversification rate metrics.

While our results are consistent with the hypothesis that behaviour drives evolution, they raise important questions about its underlying mechanisms. Specifically, there seems to be support that this association could be an effect of behavioural flexibility dampening extinction of young lineages, rather than accelerating diversification via splitting of behaviourally shifted individuals/populations as previously suggested (Wilson, 1985). If true, this would be informative in helping biologists anticipate how different organisms (i.e. flexible versus inflexible) might be expected to respond to external change (e.g. habitat modification) and, in turn, could allow biologists to better anticipate which species might be particularly vulnerable to extinction in a changing world.

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Data and code will be made available through Dryad or a similar repository.

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