



RESEARCH ARTICLE

The role of brain size on mammalian population densities

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Handling Editor: Hannah White

Abstract

1. The local abundance or population density of different organisms often varies widely. Understanding what determines this variation is an important, but not yet fully resolved question in ecology. Differences in population density are partly driven by variation in body size and diet among organisms. Here we propose that the size of an organism's brain could be an additional, overlooked, driver of mammalian population densities.
2. We explore two possible contrasting mechanisms by which brain size, measured by its mass, could affect population density. First, because of the energetic demands of larger brains and their influence on life history, we predict mammals with larger relative brain masses would occur at lower population densities. Alternatively, larger brains are generally associated with a greater ability to exploit new resources, which would provide a competitive advantage leading to higher population densities among large-brained mammals.
3. We tested these predictions using phylogenetic path analysis, modelling hypothesized direct and indirect relationships between diet, body mass, brain mass and population density for 656 non-volant terrestrial mammalian species. We analysed all data together and separately for marsupials and the four taxonomic orders with most species in the dataset (Carnivora, Cetartiodactyla, Primates, Rodentia).
4. For all species combined, a single model was supported showing lower population density associated with larger brains, larger bodies and more specialized diets. The negative effect of brain mass was also supported for separate analyses in Primates and Carnivora. In other groups (Rodentia, Cetartiodactyla and marsupials) the relationship was less clear: supported models included a direct link from brain mass to population density but 95% confidence intervals of the path coefficients overlapped zero.
5. Results support our hypothesis that brain mass can explain variation in species' average population density, with large-brained species having greater area requirements, although the relationship may vary across taxonomic groups. Future research is needed to clarify whether the role of brain mass on population density varies as a function of environmental (e.g. environmental stability) and biotic conditions (e.g. level of competition).

KEYWORDS

body mass, body size, brain mass, comparative methods, diet, Mammalia, phylogenetic path analysis, population abundance

1 | INTRODUCTION

Ecologists observed long ago that different organisms occupy natural environments at different population densities, yet what determines population density is still considered one of the unresolved problems in ecology (Dobson et al., 2020). Earlier studies proposed variation in population density among species could be explained by a combination of species' energy requirements and the availability and accessibility of resources (Brown, 1995; Damuth, 1981). These proposed relationships led to a pursuit of general rules linking interspecific variation in population density with energy requirements (White et al., 2007). Because directly measuring energy requirements across numerous species is challenging, macroecological research has relied on proxies, primarily body mass and to a lesser extent diet composition, to test these hypotheses (Damuth, 1981; Silva et al., 2001). For example, the 'energy equivalence rule' proposes that population density decreases with body mass with a power exponent of -0.75 , which is the reciprocal of the rate by which individual metabolic rates increase with body size (Damuth, 2007; White et al., 2007). This rule and its proposed exponent have been challenged on theoretical and empirical grounds (Blackburn & Gaston, 1999; Isaac et al., 2013), with research showing that the power exponent varies across taxonomic groups (Isaac et al., 2011; Pedersen et al., 2017). However, the fact that an average species' population density is associated with its average body mass remains largely supported (Isaac et al., 2011; Santini, Isaac, Maiorano, et al., 2018). Everything else equal, a larger organism will require a larger area than a smaller organism to meet its energetic requirements. In addition, energy requirements can also depend on the composition of an organism's diet for two reasons. First, animals that consume less abundant and more scattered resources are expected to need larger areas to fulfil their requirements. Second, different diet items are associated with different availabilities, foraging costs and energy assimilation efficiencies (Silva et al., 1997). For example, mammals with more nectivorous and more carnivorous diets have higher energy requirements (Anderson & Jetz, 2005; Nagy et al., 1999).

In mammals, energetic requirements are also influenced by brain size (Herculano-Houzel, 2011; Mink et al., 1981). Empirical data shows that cerebral energy use increases more steeply with brain size than whole-body energy use does with increased body size (Karbowski, 2007) such that species with larger brains have higher metabolic rates after controlling for allometric effects (Hofman, 1983; Isler & van Schaik, 2006). Brains are also costly to develop, and species with larger brains generally have reduced reproductive output and longer development times, which result in slower potential population growth rates and lower abundance (Barton & Capellini, 2011; Gonzalez-Voyer et al., 2016; Isler & van Schaik, 2009). Despite the extensive evidence that brain size influences energy requirements, the potential role of brain mass as

a predictor of average population densities has remained largely unexplored, possibly due to its high correlation with body mass and reduced availability of brain size estimates. A recent study evaluating extinction risk among mammals suggested a possible direct negative relationship between brain size and population density (Gonzalez-Voyer et al., 2016). Yet, this link was not further explored, and that study did not account for other known drivers of population density such as diet composition. In addition to the energy effect, brain size could influence population density but show a positive relationship. Larger brains have been linked to greater cognitive ability and innovation capacity, which could provide a competitive advantage over other species, including greater ability to locate ephemeral food patches and use more diverse resources in an environment, and provide advantages in coping with new conditions (Amiel et al., 2011; Maklakov et al., 2011; Santini et al., 2019; Sol et al., 2002; Visalberghi et al., 1995).

Here, we explore these hypotheses to understand the role of brain size on mammalian population densities. Because brain mass can influence energy requirements and cognitive abilities, we expect brain mass to have a direct effect on population density when also considering the effects of body mass and diet composition. If brain size primarily reflects energy requirements, larger brains should lead to lower population densities. However, if the benefits provided by larger brains in the form of greater ability to exploit available resources compensate the increased energy requirements, larger-brained species should occur at higher population densities. We test these predictions using Phylogenetic Path Analysis (PPA, Gonzalez-Voyer & von Hardenberg, 2014; von Hardenberg & Gonzalez-Voyer, 2013). This method tests multivariate hypotheses (Shibley, 2000) simultaneously solving multiple, related equations that represent direct and indirect relationships among traits, and accounts for potential issues of non-independence in trait data due to shared ancestry (Felsenstein, 1985; Martins & Hansen, 1997). Solving multiple, related equations was key in our study because the tested determinants of population density also influence each other. Brain mass has a strong allometric relationship with body mass (Striedter, 2005), and larger brain sizes have been linked to diet; for example, in primates those with more frugivorous diets have relatively larger brains (DeCasien et al., 2017). Diet is also linked to body mass with more carnivorous or folivore mammals being larger than those that feed on fruits, nectar and seeds (Pineda-Munoz et al., 2016). Considering these relationships, we proposed and compared twelve models (hypotheses) representing different related equations linking diet composition (focusing on percentage of animal items—carnivorous diets, and percentage of specialized plant items: fruit, nectar and seed), body mass, brain mass and population density (Figure 1). We compared model fit and estimated path coefficients to determine which relationships were best supported.

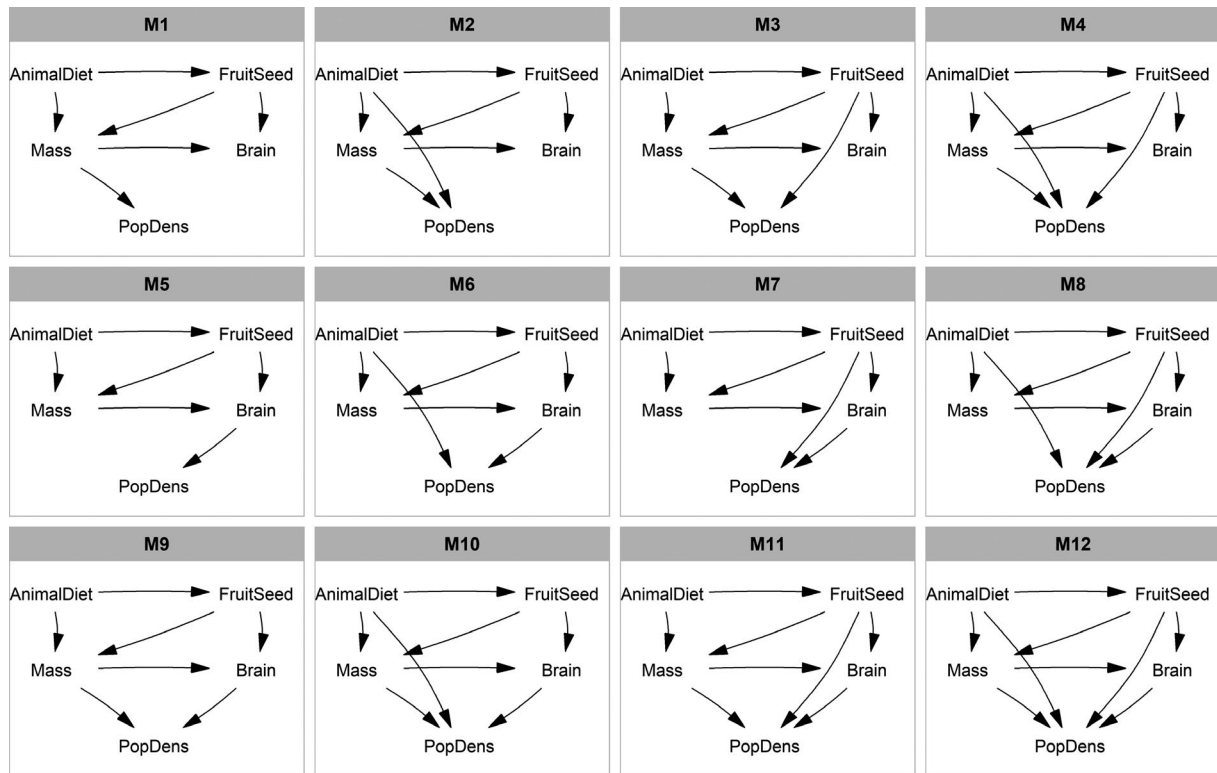


FIGURE 1 Direct acyclic graphs (DAGs) of the proposed complete path models to explore the effect of diet composition, brain and body mass on population density in non-volant terrestrial mammals. Diet composition is represented by two variables, AnimalDiet: the percentage of the diet represented by all animal items, and FruitSeed: percentage of the diet represented by fruit, nectar and seed. Relationships between diet and mass reflect those supported for all species analysed together (see Section 2 and Figures S1 and S2)

2 | MATERIALS AND METHODS

2.1 | Data compilation

We searched the literature, largely focusing on previously published compilations of data from the primary literature, to obtain estimates of population density, body mass and brain mass for different mammalian species (full dataset available in Figshare repository <https://doi.org/10.6084/m9.figshare.12867305.v1>). Population density estimates were primarily obtained from two recent compilations of individual study/population records (Novosolov et al., 2017; Santini, Isaac, & Ficetola, 2018). These compilations often included multiple records per species from which we calculated mean densities per species after removing values representing introduced and re-introduced populations and duplicates (identical values assumed to represent the same original data). Data gaps were then filled with species-average estimates of population density from other published compilations (details in Supporting Information). Body and brain mass estimates were compiled from available species-level averages in which individual measurements and sample sizes were rarely reported. We calculated the median value from the available entries after removing identical values, i.e. duplicates (dataset including all individual records available in the Figshare repository <https://doi.org/10.6084/m9.figshare.12867305.v1>). For many species we had a single estimate of body and brain mass (157 and 208 respectively). For the remaining species the mean

number of records was 6.7, with a range from 2 to 98 for body mass and 7.6 records (range 2–103) for brain mass. For species with multiple estimates we calculated variation among available estimates as the percentage difference for each record to the calculated species median: $(\text{record value} - \text{median}) \times 100 / \text{median}$. Averaging across species the median percentage difference was 10.8% for body mass and 4.7% for brain mass. We used this information during the initial data curation process to detect several errors when compiling sources (corrections are described in the compilation scripts available at the Figshare repository <https://doi.org/10.6084/m9.figshare.12867305.v1>) and afterwards to complete sensitivity analyses (see below).

Diet composition was defined using semi-quantitative measures that reflect percentages of different item categories as described by Wilman et al. (2014). We focused on two main descriptors of diet representing compositions which have been previously linked to population density, body mass and brain mass. We defined the percentage of the diet made up by animal items (AnimalDiet) adding percentages in Wilman et al.'s (2014) categories: ectotherm vertebrates, endotherm vertebrates, fish, unknown vertebrate, insect, and scavenged material. We then defined the percentage of specialized plant diets (FruitSeed) adding the percentages of three categories: fruit, nectar, and seed. We also tested alternative descriptors of animal diet based on the percentage of insects, and the sum of vertebrate items (categories: ectotherm vertebrates, endotherm vertebrates, fish, unknown vertebrate, and scavenged material—assuming

scavenging is mostly of vertebrate remains), as well as two alternative descriptors of plant items based on the percentage in the plant (leaves) category, and the seed category alone. We only included empirical diet data, excluding all values imputed based on genus or family information. To define phylogenetic relationships we used the phylogeny in Hedges et al. (2015).

2.2 | Data analyses

We proposed and tested several possible models describing different direct and indirect relationships among variables using phylogenetic path analysis (von Hardenberg & Gonzalez-Voyer, 2013). To limit the number of models to compare, we first defined the relationships between diet composition (variables AnimalDiet and FruitSeed), body and brain mass (Figure S1; Table S1). All tested diet-mass models included a direct link between the two diet variables because these represent percentages of the same total and thus are by definition linked, and a direct effect of body mass on brain mass to reflect their strong allometric relationship. We used the best-supported diet-mass model as the basis to explore a series of complete models linking diet and mass to population density (Figure 1). In PPA the links must be directional, in the main results we assumed that the directionality in diet was from AnimalDiet to FruitSeed. The Supporting Information show results were qualitatively the same assuming the alternative direction (Table S2).

All models were fitted and compared using phylogenetic path analysis as implemented in the package `PHYLOPATH` (van der Bijl, 2017) in R3.6.1 (R Development Core Team, 2019). Prior to analyses we \log_{10} -transformed body mass, brain mass and population density, and then scaled all variables (subtracting the mean and dividing by the standard deviation). Because variables are scaled, path coefficients are directly comparable in magnitude. We compared models using the C statistic information criterion CIC (von Hardenberg & Gonzalez-Voyer, 2013). Model averaging was used when possible to incorporate uncertainty in model selection, but defining the complete model required a single diet-mass model (a unique set of links). We defined the best-supported diet-mass model as the one with lowest CIC if a single model was supported (single model with $\Delta\text{CIC} < 2$). When multiple models were supported we considered the simplest (fewer links) supported model with proposed links between variables having 95% confidence intervals not overlapping with zero. For complete models linking diet and mass to population density, if several models were supported ($\Delta\text{CIC} < 2$) we used conditional model averaging to calculate path coefficients and their 95% confidence intervals. We averaged across models that included direct links, met conditional independences and had $\Delta\text{CIC} < 2$ using the function 'average' from the `PHYLOPATH` package. When a single model was supported we calculated path coefficients and bootstrapped 95% confidence intervals (based on 5,000 replicates) using the package `PHYLOLM` (Tung Ho & Ané, 2014). We analysed all available data combined (all-data model), and completed separate analyses to evaluate group-specific patterns for taxonomic orders with data for at least 80 species (Primates, Rodentia, Cetartiodactyla and Carnivora) and for marsupials (Infraclass Metatheria, including species from the

taxonomic orders *Dasyuromorphia*, *Didelphimorphia*, *Diprotodontia* and *Peramelemorphia*). Because we only included terrestrial species, to avoid confusion, hereafter we refer to *Cetartiodactyla* by the former order name *Artiodactyla*. Scripts of the analyses are available at the Figshare repository <https://doi.org/10.6084/m9.figshare.12867305.v1>.

Comparative analyses have traditionally explored the role of brain mass using residuals obtained from a log-log brain to body mass regression to capture 'relative brain effects', even though, the use of residuals leads to biased parameter estimates (Freckleton, 2002; García-Berthou, 2001). For comparison we present a supporting analysis based on brain residuals and Phylogenetic Generalized Least Squares (Supporting Information: Supplementary analyses).

3 | RESULTS

3.1 | Representation of extant mammalian diversity in the dataset

We found trait and phylogenetic data for 656 terrestrial non-volant mammals. As expected data were not available for all species, nor did the available data represent a random subset of the mammalian diversity, which is a common issue in comparative studies (González-Suárez et al., 2012). While the data are not a random sample of all mammals, the dataset included species from 20 taxonomic orders and 92 families (Figure 2), which spanned several orders of magnitude in body mass, brain mass and population density, and also represented the entire range of diet categories (Figures S3–S5). There were varying levels of correlation among variables, with body mass and brain mass being most strongly correlated, as expected (Figure S6).

3.2 | Relationships between brain mass, body mass and diet categories

The best-supported model describing relationships between brain, body mass and diet for all species included direct effects of AnimalDiet and FruitSeed (diet variables) on body mass and a direct effect of

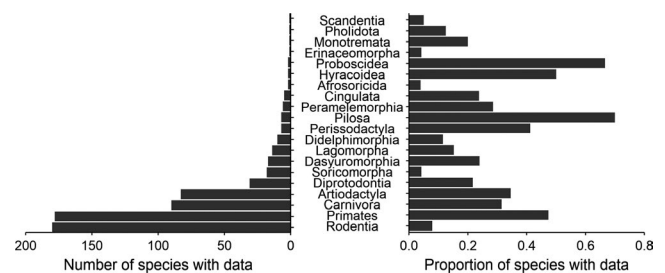


FIGURE 2 Data availability as total number of species per order and the proportion of species in each order included in the analysed dataset ($N = 656$ species). The comparison shows that representation varied with some species-poor orders like Proboscidea well-represented, but relatively poor coverage of species-rich orders like Rodentia

the percentage of the diet composed by fruits, nectar and seeds (FruitSeed) on brain mass (Figure S2; Table S1). Alternative diet variables supported the same model structure (Table S1). When considering separate species groups (Primates, Rodentia, Carnivora, Artiodactyla and marsupials) we found varying relationships between diet and brain mass among groups, with overall consistent results when exploring alternative diet variables (Tables S3–S7; Figure S2).

3.3 | Brain mass and population density

The single best-supported complete model for all species (M12, Figure 1) included direct links from both diet variables, brain mass and body mass to population density (Table 1). Path coefficient estimates (Figure 3) showed that lower population densities occur in species with larger brain mass and those that consume diets with

TABLE 1 Model comparison for hypothesized relationships between diet, mass and population density for non-volant terrestrial mammalian species (models for all species together and for groups tested separately). Diet is represented by percentage of animal items on the diet (AnimalDiet), and by percentage of the diet composed of fruits, nectar and seeds (FruitSeed). Supported models used to estimate patch coefficients (Figure 2) are in bold. We report *k*: number of independence claims, *q*: number of parameters, *C*: Fisher's *C* statistics, CICc: C statistic Information Criterion corrected for small sample sizes, ΔCICc: difference in CICc from the best-fitting model, *w*: CICc weights

Model	Diet direct effects	Mass direct effects	<i>k</i>	<i>q</i>	<i>C</i>	<i>p</i>	CICc	ΔCICc	<i>w</i>
All species (<i>N</i> = 656)									
M12	AnimalDiet and FruitSeed	Body and brain	1	14	3.99	0.14	32.64	0.00	0.75
M8	AnimalDiet and FruitSeed	Brain	2	13	9.35	0.05	35.92	3.28	0.15
M4	AnimalDiet and FruitSeed	Body	2	13	10.50	0.03	37.07	4.43	0.08
M10	AnimalDiet	Body and brain	2	13	13.77	0.01	40.34	7.70	0.02
M6	AnimalDiet	Brain	3	12	16.63	0.01	41.11	8.47	0.01
Rodentia (<i>N</i> = 180)									
M12	AnimalDiet and FruitSeed	Body and brain	1	14	3.50	0.17	34.05	0.00	0.42
M4	AnimalDiet and FruitSeed	Body	2	13	5.86	0.21	34.05	0.01	0.42
M8	AnimalDiet and FruitSeed	Brain	2	13	7.87	0.10	36.06	2.02	0.15
M11	FruitSeed	Body and brain	2	13	15.91	0.00	44.10	10.06	0.00
M7	FruitSeed	Brain	3	12	18.27	0.01	44.14	10.09	0.00
Primates (<i>N</i> = 178)									
M8	AnimalDiet and FruitSeed	Brain	3	12	3.32	0.77	29.21	0.00	0.40
M12	AnimalDiet and FruitSeed	Body and brain	2	13	2.49	0.65	30.71	1.49	0.19
M4	AnimalDiet and FruitSeed	Body	3	12	4.94	0.55	30.83	1.62	0.18
M6	AnimalDiet	Brain	4	11	9.07	0.34	32.66	3.45	0.07
M5	None	Brain	5	10	12.04	0.28	33.36	4.15	0.05
Carnivora (<i>N</i> = 90)									
M3	FruitSeed	Body	4	11	4.39	0.82	29.77	0.00	0.35
M7	FruitSeed	Brain	4	11	6.10	0.64	31.48	1.71	0.15
M4	AnimalDiet and FruitSeed	Body	3	12	3.73	0.71	31.78	2.01	0.13
M2	AnimalDiet	Body	4	11	6.72	0.57	32.10	2.33	0.11
M11	FruitSeed	Body and brain	3	12	4.05	0.67	32.11	2.33	0.11
Artiodactyla (<i>N</i> = 83)									
M3	FruitSeed	Body	3	12	3.11	0.79	31.57	0.00	0.30
M7	FruitSeed	Brain	3	12	3.57	0.73	32.03	0.46	0.24
M4	AnimalDiet and FruitSeed	Body	2	13	2.58	0.63	33.85	2.28	0.10
M8	AnimalDiet and FruitSeed	Brain	2	13	2.72	0.61	34.00	2.43	0.09
M11	FruitSeed	Body and brain	2	13	3.08	0.54	34.35	2.78	0.08
Marsupials (<i>N</i> = 64)									
M6	AnimalDiet	Brain	4	11	4.33	0.83	31.41	0.00	0.28
M2	AnimalDiet	Body	4	11	4.62	0.80	31.70	0.29	0.25
M4	AnimalDiet and FruitSeed	Body	3	12	2.33	0.89	32.45	1.04	0.17
M10	AnimalDiet	Body and brain	3	12	3.20	0.78	33.31	1.90	0.11
M8	AnimalDiet and FruitSeed	Brain	3	12	3.41	0.76	33.53	2.12	0.10

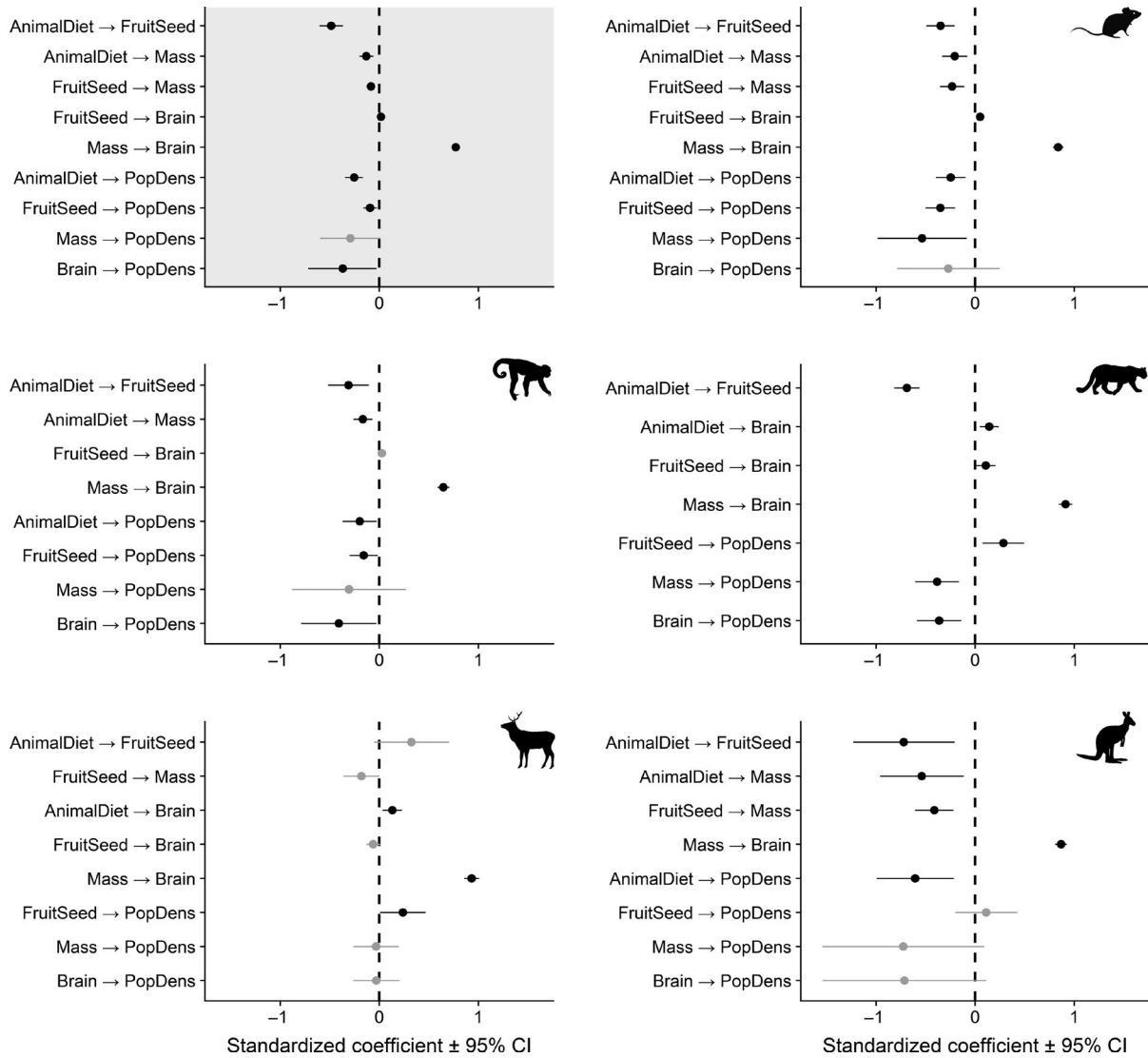


FIGURE 3 Standardized path coefficients (with 95% confidence intervals) estimated from the single supported model (for all species, grey background panel) or using model averaging from supported ($CIC < 2$) models for tested groups (Table 1). Relationships with 95% confidence intervals not overlapping with zero are shown in black, those overlapping zero are in grey. In some cases 95% CI were very narrow and lines are not visible. Top left panel with grey background shows results for all 656 non-volant terrestrial mammals, other panels show results for groups tested separately (from top to bottom: rodents, primates, carnivorans, ungulates (Artiodactyla) and marsupials). Figure 1 illustrates the model diagrams. Variables are: AnimalDiet: percentage of the diet composed by animal items; FruitSeed: percentage of the diet composed by fruits, nectar and seeds, Mass: average adult body mass; Brain: average adult brain mass; PopDens: average population density

higher percentages of animal items or higher percentages of fruits, nectar and seeds. A direct link between body mass and population density was included in the supported model with a negative path coefficient, but 95% confidence intervals slightly overlapped zero (best estimate = -0.29 , 95% CI: $-0.600, 0.015$).

Analyses for separate groups showed group-specific idiosyncrasies. We found that primates and carnivorans with larger brains live at lower densities (Figure 3), but the effect was not clear for rodents, ungulates (order Artiodactyla) and marsupials. Similarly, carnivorans and rodents with larger body mass live at lower population densities, but for primates, ungulates or marsupials the effect was not clear. Unclear effects occurred when one or more of the supported

models included the direct link between brain mass or body mass and population density, but the bootstrapped estimates of the 95% confidence intervals of those path coefficients overlapped zero. In carnivorans both body and brain mass were linked to population density, but contrary to the results from all species in which the only supported model included both direct links, for this group results reflected model averaging of two supported models in which either body mass or brain mass was associated to population density (Table 1). Diet was associated with density in all groups with negative effects of both AnimalDiet and FruitSeed in rodents and primates, positive effects of FruitSeed on carnivorans and ungulates and negative effects of AnimalDiet on marsupials.

4 | DISCUSSION

Our results show a negative direct link between average species brain mass and population density in mammals. The link was detected when analysing all 656 species together and clearly supported in separate analyses for primates and carnivorans. For all species and primates supported models included direct links from both body mass and brain mass to population density, although non-significant path coefficients indicate a less clear effect of body mass. Support for models that include both direct links suggests brain and body mass estimates could reflect distinct types of drivers or trade-offs. In carnivorans, the two supported models included a direct link from either body mass or brain mass to population density, possibly indicating a more general body size effect on population density where size could be represented by total mass or partial (brain) mass.

The identified links between brain mass and population density are consistent with the hypothesis that higher energetic requirements for species with larger relative brain size lead to lower population densities. Relatively large brains have also been associated with higher cognitive capacity (Benson-Amram et al., 2016; Reader & Laland, 2002; Sol et al., 2005), which we hypothesized could counterbalance energetic requirements by making individuals better at exploiting resources. While brain size has been linked to species adaptability to novel conditions in mammals (Santini et al., 2019; Sol et al., 2008), our results do not support the hypothesis that this benefit compensates the higher energy costs of a larger brain, although this is likely the case for some species such as humans (Navarrete et al., 2011). While our findings are consistent with the proposed hypothesis, there could be an alternative, methodological, explanation for a link between brain mass and population density. Brain mass is less variable than body mass during the adult life span in mammals and thus, brain mass could act as a more accurate estimate of the species' average adult size rather than an indicator of additional energy requirements. We completed sensitivity analyses to test this explanation that show our findings cannot be explained solely based on brain mass being a more accurate estimate of size (Supporting Information: Supplementary analysis, Table S9). We also tested sensitivity of our results to variation in population density and similarly found results to be robust to potential error in density estimates (Table S9).

Our results could also be consistent with another biological mechanism linking brain size and population density. Larger brains can be associated with more complex social systems (the social brain hypothesis: Dunbar, 1998); in these social systems, cooperative group members have the ability to defend much larger territories than the area needed to fulfil the energy requirements of the group (Shultz & Dunbar, 2006). Within particular species, there is evidence of groups with more complex social structures defending larger (per capita) territories (Pasquaretta et al., 2015). Whether territoriality leads to population densities in large-brained social species being lower than expected based only on energy requirements is an intriguing hypothesis that could be explored in future studies. A limitation to such studies is that data on social complexity are sparse and difficult to obtain. Potential proxies, like group size, do not truly

capture social complexity across mammalian species (e.g. an ungulate herd may be very large but does not have the social cohesion of a smaller primate troop).

As found in previous research (Silva et al., 1997) our analyses link population density with diet. Overall, our results are consistent with a more specialized diet (higher percentages of the diet made up of animal items or specialized plant materials: fruits, nectar and seeds) being associated with lower population densities for all mammals, rodents, primates and marsupials. On the other hand, for carnivorans and ungulates, consuming more specialized plant materials (fruits, nectar and seeds) was associated with higher population densities. Because most carnivorans have animal-based diets, those consuming more fruits, nectar and seeds (e.g. kinkajou *Potos flavus*) are effectively less specialized, a result consistent with the general pattern that less specialized diets are associated to larger densities. Similarly, most ungulates are folivores, and those that consume fruits and seeds may be considered less specialized.

While not the main focus of the study, our results also show interesting relationships between diet composition and brain mass. When analysing all species together we found mammals consuming more fruits, nectar and seeds had larger brain mass and the same results held for rodents, carnivorans and ungulates. However, in marsupials smaller brains were associated with this specialized diet. Consuming more animal-based diets was associated with larger brains in carnivoran and ungulate species. Contrary to previous work (DeCasien et al., 2017), we did not find a significant link between larger primate brain mass and diets with more fruits, nectar and seeds, although there was a positive trend (best estimate = 0.025, 95% CI: -0.003, 0.053). Differences may reflect different samples (we included an additional 36 primate species), a different source for diet data, and/or a different analytical approach and phylogeny. Overall, our results suggest that within trophic groups, diets specialized in items that require searching and 'capture' (hunting prey or fruit locating and picking) may require more complex behaviours and greater cognitive capacities resulting in larger brain sizes.

Our study shows that mammalian population density is affected by both brain and body mass. Previous research on interspecific patterns associating mass and population density has focused on total body mass estimates, but our findings suggest that considering both brain and body mass together (or testing them as alternatives) could offer additional information, lead to better predictive models and reveal groups, such as primates, for which population density may be best explained by brain size. We acknowledge testing both currently presents a challenge because while empirical estimates of body mass are available for nearly 4,900 mammals (Faurby et al., 2018) brain data are available for considerably fewer species (~1,500 mammals, Tsuboi et al., 2018). Extending the collection of brain mass data would aid future comparative analyses.

Vertebrates with larger brain sizes have been shown to be more successful under certain environments and conditions (Amiel et al., 2011; Maklakov et al., 2011; Santini et al., 2019; Sol et al., 2002, 2008). However, here (and in previous research: Gonzalez-Voyer et al., 2016)

we show larger brains also entail ecological costs. Our findings open future avenues of research exploring the nuances of how brain size influences population density under different environmental and biotic conditions. Relatively larger brains generally lead to lower population density, but larger brains could allow some species to live at higher densities than expected under challenging or novel conditions. A relatively large brain may provide benefits in the form of more complex social and behavioural strategies that allow species to cope with highly seasonal or unpredictable environments, or to out-compete other species and/or reduce their vulnerability to predators in communities with higher competition and predation pressure. Alternatively, a relatively larger brain might not be associated with higher population densities, but could allow species to persist in a wider array of abiotic and biotic conditions at the cost of lower population densities. These are questions that will help us further understand the role of brain mass in species' ecology and evolution, and how brain size influences a species' abilities to cope with global change.

ACKNOWLEDGEMENTS

We thank Isabella Capellini for suggesting the social hypothesis under which larger brain size could lead to higher population densities. Credits for silhouettes in figures: Sarah Werning for *Cebus albifrons* (White-fronted capuchin), Daniel Jaron for *Mus musculus* (house mouse), Steven Traver for *Cervus elaphus* (red deer), 'An Ignorant Atheist' for *Puma concolor* (cougar), Cathy for *Macropus rufus* (red kangaroo). All silhouettes were downloaded from PhyloPic (<http://phylopic.org/>) and represent species in our dataset.

AUTHORS' CONTRIBUTIONS

M.G.-S. and A.G.-V. conceived the study; all authors designed it and interpreted results; M.G.-S. and L.S. compiled the data; M.G.-S. completed all analyses and lead the writing, with contributions from all authors.

DATA AVAILABILITY STATEMENT

All data and R scripts (for data compilation and data analyses) are available on the Figshare repository <https://doi.org/10.6084/m9.figshare.12867305.v1>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: González-Suárez M, Gonzalez-Voyer A, von Hardenberg A, Santini L. The role of brain size on mammalian population densities. *J Anim Ecol*. 2020;00:1–9. <https://doi.org/10.1111/1365-2656.13397>