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Is group size related to longevity in mammals?

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Life-history theory predicts that reduced extrinsic risk of mortality should increase species longevity over evolutionary time. Increasing group size should reduce an individual's risk of predation, and consequently reduce its extrinsic risk of mortality. Therefore, we should expect a relationship between group size and maximum longevity across species, while controlling for well-known correlates of longevity. We tested this hypothesis using a dataset of 253 mammal species and phylogenetic comparative methods. We found that group size was a poor predictor of maximum longevity across all mammals, as well as within primates and rodents. We found a weak but significant group-size effect on artiodactyl longevity, but in a negative direction. Body mass was consistently the best predictor of maximum longevity, which may be owing to lower predation risk and/or lower basal metabolic rates for large species. Artiodactyls living in large groups may exhibit higher rates of extrinsic mortality because of being more conspicuous to predators in open habitats, resulting in shorter lifespans.

Keywords: lifespan; senescence; life history; predation; sociality

1. INTRODUCTION

Broad-scale quantitative examinations of the ultimate causes of lifespan variation have received little attention until recently. Several comparative studies of different vertebrate groups have confirmed that body size and age at first reproduction are important predictors of longevity (Gaillard *et al.* 1989), but they have also examined the potential significance of additional variables, such as arboreality in mammals (Shattuck & Williams 2010) and group size in birds (Blumstein & Møller 2008; Beauchamp 2010). Spending more time in trees and living in larger groups should lower extrinsic mortality by reducing predation risk. In addition, group living is often believed to reduce starvation by increasing access to food resources and increasing cooperation among individuals (Alexander 1974; Clutton-Brock 2002). Group living may also have costs, such as increasing feeding competition (Molvar & Bowyer 1994) or being more conspicuous to predators (Ebensperger & Blumstein 2006).

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Species suffering high extrinsic mortality rates should have shorter lifespans because they apportion more energy into reproducing quickly and use less energy for long-term maintenance and survival (Austad & Fisher 1991; Wilkinson & South 2002). Thus, life-history theory predicts that species should increase lifespan over evolutionary time when extrinsic mortality levels are low. Ricklefs (2008) argued that there should be strong selection for removing genetic variants that reduce lifespan, with most mortality being attributed to intrinsic ageing-related death. Similarly, when extrinsic mortality is low, mutations benefiting an individual early in life and causing deleterious effects late in life may be selected for (Williams 1957).

Recent investigations of the potential relationship between group size and longevity have been mixed. In comparative studies, Munshi-South & Wilkinson (2006) and Beauchamp (2010) found no relationship between group size and longevity in birds. Also, Blumstein & Møller (2008) found no relationship between the degree of cooperative care and cooperative breeding and lifespan in North American birds. By contrast, Wasser & Sherman (2010) found that social breeding was positively related to increased longevity in over 900 bird species, but they did not employ phylogenetic comparative methods or control for sampling effort. In addition, Jullien & Clobert (2000) showed that Neotropical bird species living in obligate flocks displayed higher survival rates compared with species that foraged alone or in pairs. Although survival rates are not synonymous with longevity, there should be a strong relationship between the two.

In this current analysis, we build on recent studies by investigating the possible effect of group size on mammalian longevity, while simultaneously accounting for additional well-known or potential correlates of lifespan.

2. MATERIAL AND METHODS

We gathered data from published databases for 253 mammal species representing 18 orders (Jones *et al.* 2009; Shattuck & Williams 2010; electronic supplementary material). We used maximum longevity as our dependent variable and 10 predictor variables. In addition to examining group size, we needed to account for additional variables that probably affect variation in longevity (Gaillard *et al.* 1989; Blumstein & Møller 2008; Beauchamp 2010). For each species, we gathered data on: (i) median social group size, (ii) median adult body mass, (iii) median age at sexual maturity, (iv) mean monthly temperature, (v) mean monthly precipitation, (vi) mid-latitude (absolute values) of their range, (vii) mean human population density, (viii) degree of arboreality, (ix) longevity and (x) group-size sample size (i.e. sampling effort). Arboreality was not used in the artiodactyl analysis because all species are terrestrial. Following previous studies (Kamilar & Paciulli 2008; Kamilar 2009), we used several environmental variables as proxies for habitat characteristics, and consequently the selective environment that species are subjected to.

All variables, but arboreality, were log transformed prior to analysis. We used phylogenetically independent contrasts to account for the shared evolutionary history of species (Felsenstein 1985). To calculate the contrasts, we used a recently published mammal supertree (Bininda-Emonds *et al.* 2007) and set all branch lengths equal to one to better meet the assumptions of independent contrasts (Garland *et al.* 1992). All contrasts were calculated with PDAP for MESQUITE (Maddison & Maddison 2007).

We analysed four different datasets: (i) all mammals, (ii) primates, (iii) rodents and (iv) artiodactyls. This allowed us to better examine potential differences among these clades (Gaillard *et al.* 2003). The primates, rodents and artiodactyls were the only orders with a sufficient sample size to conduct separate analyses.

Table 1. Full model multiple regressions predicting maximum longevity using phylogenetically independent contrasts.

predictors	all mammals ^a		primates		artiodactyls ^{a,b}		rodents	
	β	p	β	p	β	p	β	p
body mass	0.563	<0.001	0.441	<0.001	0.604	<0.001	0.687	0.001
group size	-0.064	0.165	0.132	0.107	-0.262	0.027	0.124	0.627
arboreality	0.232	<0.001	0.204	0.022	—	—	0.348	0.187
age at sexual maturity	0.140	0.016	0.155	0.103	0.139	0.264	0.087	0.679
human population density	-0.017	0.757	-0.045	0.621	0.306	0.089	0.034	0.868
mean temperature	0.134	0.014	0.141	0.113	-0.231	0.204	0.011	0.961
mean rainfall	-0.113	0.046	0.158	0.085	-0.049	0.739	-0.313	0.152
absolute latitude	0.017	0.743	0.248	0.019	-0.101	0.451	-0.284	0.255
longevity sample size	0.224	<0.001	0.364	<0.001	0.137	0.189	0.061	0.764
group-size sample size	0.018	0.699	0.071	0.422	0.023	0.824	-0.150	0.473
total model results	$r^2 = 0.552, p < 0.001, \text{d.f.} = 10,237$		$r^2 = 0.501, p < 0.001, \text{d.f.} = 10,79$		$r^2 = 0.455, p < 0.001, \text{d.f.} = 9,59$		$r^2 = 0.629, p = 0.006, \text{d.f.} = 10,21$	

^aResults presented without outliers.

^bAll artiodactyl species are terrestrial.

Table 2. Best predictor variables of maximum longevity based on AIC. (Variables occurring in 100% of the set of 'best' models are the strongest predictors. Models within 2 AIC units of the 'best' model are considered equally good (Burnham & Anderson 2003). Number of 'best' models for: mammals, 6; primates, 10; artiodactyls, 22; rodents, 7. See electronic supplementary material for more detailed results of the AIC analyses.)

predictors	per cent of occurrence in the set of best models			
	all mammals	primates	artiodactyls	rodents
body mass	100	100	100	100
group size	33	80	91	14
arboreality	100	100	—	100
age at sexual maturity	100	70	32	0
human population density	17	10	45	14
mean temperature	100	70	27	14
mean rainfall	100	60	9	100
absolute latitude	0	90	9	100
longevity sample size	100	100	45	14
group-size sample size	33	10	9	14

For each dataset, we initially conducted a multiple linear regression using all predictor variables to examine the potential presence of outliers. We identified extreme outliers as contrasts that exhibited a studentized residual of $>+3$ or <-3 . We re-ran any datasets that initially contained outliers. In addition, we used Akaike's information criterion (AIC) to determine the best subset of variables that explained longevity. Models within 2 AIC units of the best model are considered equally good (Burnham & Anderson 2003). Variables that were present in all of the equally good models were the strongest predictors of longevity.

All analyses were conducted with STATISTICA and used a zero intercept model, which is a requirement of independent contrasts (Felsenstein 1985).

3. RESULTS

The multiple regression analyses including all independent variables were statistically significant for all datasets, yet many variables differed in their importance for predicting longevity (table 1 and electronic supplementary material). We found that group size was not significantly positively related to maximum longevity using any dataset. By contrast, there was a significant negative effect of group size on artiodactyl longevity ($\beta = -0.262, p = 0.027$). Body mass was

positively and significantly related to longevity for all datasets. In addition, arboreality was positively related to longevity for all mammals and primates. Human population density and group-size sample size were not significant predictors for any dataset. The remaining variables were important predictors of longevity in some datasets and not others.

Using AIC, six equally-good models were produced for the total mammal dataset, 10 for the primate dataset, 22 for the artiodactyl dataset and seven for the rodent dataset (electronic supplementary material). The presence of individual predictor variables in these best models mostly corroborated the multiple regression results. Body mass and arboreality were the only variables entered into all of the best models (table 2). There was some support for a group-size effect on artiodactyl longevity, being present in 20 out of 22 of the best models. The remaining variables differed in their ability to predict longevity, depending on the dataset.

We found outliers in the all mammals and artiodactyls datasets, but none for the primates and rodents (electronic supplementary material).

4. DISCUSSION

We found little evidence to support the idea that mammal species living in larger social groups exhibit longer lifespans when controlling for other factors known to influence longevity. These results were consistent across all mammals, as well as within primates and rodents separately. Interestingly, the artiodactyls displayed a weak but significant group-size effect, yet in the opposite direction expected. By contrast, we found a strong and positive relationship between body mass and longevity for all datasets, confirming previous studies (Austad & Fisher 1991). One possible mechanism that might explain the body-size effect is a reduction of predation risk for large species (Werner & Gilliam 1984). Large species that have few predators or are risk averse in the presence of predators (Blumstein 2006) should have reduced extrinsic mortality and, therefore, body size should be correlated with extended lifespans. In addition, basal metabolic rate is lower in large species, and previous research has shown that metabolism is correlated with longevity (Austad & Fisher 1991).

Our non-artiodactyl results are consistent with recent studies of birds that control for phylogeny (Blumstein & Møller 2008; Beauchamp 2010), and suggest the absence of a strong group-size effect on longevity may be a broader pattern common to many vertebrates. Although several authors have argued that living in social groups confers benefits to group members, consequently reducing mortality rates, other research suggests that there are negative aspects of living in large social groups. This may help to explain our artiodactyl results. Individuals living in large social groups may suffer from increased predation risk owing to being more conspicuous (e.g. Ebensperger & Blumstein 2006). Most artiodactyls are relatively large mammals (especially, compared with rodents and primates) which may be more conspicuous to visual predators when in large social groups. The increased extrinsic mortality risk of these species would translate into faster life histories, including shorter lifespans.

In addition, several studies have shown that larger group size and/or population density is associated with higher levels of parasite infection (Altizer *et al.* 2003). However, the connection between parasite infection and mortality is not always clear. For instance, Nunn *et al.* (2003) found no relationship between parasite species richness and host longevity in a large sample of anthropoid primates, yet a significant negative relationship was found by Morand & Harvey (2000) for 23 mammal species.

Finally, species living in highly stochastic habitats should adopt faster life-history strategies and, consequently, exhibit reduced maximum longevity values (Austad & Fisher 1991). Although we accounted for average and seasonal shifts in environmental conditions, it is difficult to quantify environmental stochasticity.

In conclusion, we suggest that group size is not positively correlated with longevity for most mammals, and may actually be negatively related to longevity for some large species living in open habitats, such as many artiodactyls.

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