

Group-foraging is not associated with longevity in North American birds

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Group-foraging is common in many animal taxa and is thought to offer protection against predators and greater foraging efficiency. Such benefits may have driven evolutionary transitions from solitary to group-foraging. Greater protection against predators and greater access to resources should reduce extrinsic sources of mortality and thus select for higher longevity according to life-history theory. I assessed the association between group-foraging and longevity in a sample of 421 North American birds. Taking into account known correlates of longevity, such as age at first reproduction and body mass, foraging group size was not correlated with maximum longevity, with and without phylogenetic correction. However, longevity increased with body mass in non-passerine birds. The results suggest that the hypothesized changes in predation risk with group size may not correlate with mortality rate in foraging birds.

Keywords: body mass; group size; foraging; independent contrasts; maximum longevity; passerine versus non-passerine bird

1. INTRODUCTION

Foraging in groups occurs in many animal taxa including invertebrates, fishes, birds and mammals (Krause & Ruxton 2002). Group-foraging is thought to offer protection against predators and to increase foraging efficiency, two factors which may have favoured the evolutionary transition from solitary to group-foraging (Alexander 1974). Increased protection against predators should decrease predation risk and enhanced foraging efficiency should decrease starvation risk, thus decreasing extrinsic sources of mortality in group-foraging species. Life-history theory predicts that maximum longevity should increase when extrinsic mortality decreases (Williams 1957; Ricklefs 2008). This is because deleterious mutations that act later in life are less exposed to natural selection and thus tend to accumulate. In addition, late-acting deleterious mutations that have beneficial consequences early in life can also be selected. Therefore, species that are exposed to lesser extrinsic mortality, such as group-foraging species, would be expected to live longer (Møller 2006; Munshi-South & Wilkinson 2006; Blumstein & Møller 2008).

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Evidence for an association between maximum longevity and group-foraging is scant and indirect. In a small sample of tropical species, adult survival was found to be higher in flocking than in solitary species (Jullien & Clobert 2000). While adult survival is one component of maximum longevity, maximum longevity was not documented directly in these tropical species. In addition, it is not clear whether the results can be extrapolated to birds living in different habitats. In a more direct test, maximum flock size was not related to maximum longevity in parrots (Munshi-South & Wilkinson 2006). However, the results are difficult to interpret because not all predictive variables were analysed together and because the taxonomic focus was quite narrow. In a recent study, there was little correlation between cooperative breeding, in which groups are maintained for foraging and for reproduction, and maximum longevity (Blumstein & Møller 2008). Again these results are difficult to interpret given that the size of cooperative breeding groups was not included in the analysis and that many non-cooperative breeding species are known to forage in groups in the non-breeding season.

I evaluated the relationship between maximum longevity and group-foraging in a large dataset of North American birds including species from different habitats and different families, thus providing a wider scope to evaluate the sociality hypothesis. Evolutionary transitions to group-foraging have occurred frequently in birds, thus providing several potential contrasts between solitary and group-foraging species (Beauchamp 2002).

Maximum longevity has been related to many life-history traits and ecological factors, which must be taken into account to provide a rigorous test of the sociality hypothesis. Maximum longevity has previously been shown to increase with body mass and with age at first reproduction (Møller 2006; Speakman 2007) and historically, lifespan was thought to scale differently in passerine and non-passerine birds (Lindstedt & Calder 1976). Therefore, I assessed the sociality hypothesis using body mass, age at first reproduction and taxonomic group as cofactors. I also considered the effects of migration distance and various habitat features, which may influence starvation risk and/or predation risk (Munshi-South & Wilkinson 2006; Møller 2007).

2. MATERIAL AND METHODS

Data on maximum longevity, to the nearest month, were obtained mostly from the Patuxent Wildlife Research Center database, which provides for each species the number of birds banded, the number of recoveries and the maximum longevity recorded for birds captured in North America. In addition, I obtained some data on maximum longevity from the primary bird literature. Maximum longevity usually increases with the number of recoveries (Arnold 1988). Therefore, number of recoveries was used to adjust estimates of maximum longevity in all models. As a compromise between sample size and model estimate precision, I excluded species with fewer than 15 recoveries.

Biological data for all species were obtained from the literature (appendix A in the electronic supplementary material). Group size data during foraging often include the range but less often the mean or modal values. I therefore used the maximum group size reported during foraging. In previous work, maximum group size has been shown to be responsive to ecological factors (Beauchamp 2004). I selected data on group sizes obtained during the non-breeding season so as to avoid possible interference from parental duties. I excluded data obtained at night or during migration. Because many species join groups of other species, estimates of maximum

Table 1. Relationships between maximum longevity in birds and independent variables ($n = 421$ species and $n = 396$ contrasts).

variable	<i>F</i>	d.f.	<i>p</i>	slope or adjusted means (s.e.)	effect size (Pearson's <i>r</i>)
<i>reduced model for species</i>					
recovery number	230.5	1	<0.0001	0.11 (0.007)	0.45
body mass	25.7	1	<0.0001	0.07 (0.01)	0.15
age at first reproduction	51.9	1	<0.0001	0.05 (0.007)	0.22
order	4.8	1	0.03	non-passerine: 1.14 (0.01); passerine: 1.09 (0.02)	0.07
habitat type	6.4	1	0.01	aquatic: 1.14 (0.02); terrestrial: 1.09 (0.01)	0.08
habitat openness	3.4	1	0.06	open: 1.10 (0.01); closed: 1.13 (0.02)	0.06
migration	4.0	1	0.04	long-distance: 1.13 (0.02); not long-distance: 1.09 (0.008)	0.06
error		389			
<i>reduced model with contrasts</i>					
recovery number	278.3	1	<0.0001	0.12 (0.007)	0.61
age at first reproduction	7.5	1	0.006	0.15 (0.06)	0.10
body mass (passerines)	0.69	1	0.41	0.04 (0.05)	0.003
body mass (non-passerines)	11.6	1	0.007	0.10 (0.03)	0.13
error		398			

group sizes also included the number of heterospecifics. However, given that members of one species may be more responsive to the number of conspecifics than to the total number of companions in the group (Metcalf 1984), I also tallied the maximum number of conspecifics in groups. Number of cited references consulted was used as a cofactor because estimates of maximum group size might increase with the number of references investigated. For body mass, I used data from males in the non-breeding season, if available, because body mass in males usually shows less fluctuation throughout the year. I distinguished passerine and non-passerine species using the existing taxonomy. I classified each species as aquatic or terrestrial, depending on the main habitat used for foraging, and as foraging in open or closed habitats depending on the availability of vegetation cover during foraging activities. For migration, I distinguished long-distance migrants, which typically migrated over 30° of latitude, from short-distance or non-migrating species.

All quantitative data were \log_{10} -transformed prior to statistical analysis. I first performed a multiple regression analysis using species as the unit of analysis. The final model was obtained using backward elimination of non-significant variables. A phylogenetic analysis relied on independent contrasts, which were calculated using the PDAP module (Midford *et al.* 2008) within MESQUITE (Maddison & Maddison 2009) assigning all branch lengths to 1. The phylogeny underlying the calculations was based mostly on two recent papers describing phylogenetic relationships among bird families (Jönsson & Fjeldså 2006; Livezey & Zusi 2007). In addition, I used several papers describing interspecies relationships within various bird families (appendix B in the electronic supplementary material). Contrasts were obtained for each continuous variable. For categorical variables, I relied on ancestral state reconstruction with MESQUITE to establish the most parsimonious distribution of the trait along the phylogeny lineages. I used the same multiple regression framework to analyse the data with the restriction that the intercept must pass through the origin (Felsenstein 1985). The phylogenetic analysis was also conducted using mean or modal group sizes and the results were very similar, albeit based on a smaller sample size, and thus ignored. With the present sample size, the power was sufficient to detect small correlations (<0.1).

3. RESULTS

I uncovered data on maximum longevity for 421 North American species (appendix A in the electronic supplementary material). Maximum longevity in the full species model, taking into account the number of recoveries, was not significantly associated with maximum group size (β (s.e.) = -0.005 (0.007); $p = 0.46$;

$r = 0.02$) or with maximum conspecific group size (β (s.e.) = -0.007 (0.007); $p = 0.31$; $r = 0.03$). In the final model, in which 66 per cent of the total variation was explained, maximum longevity increased significantly with the number of recoveries, with body mass and with age at first reproduction (table 1). Maximum longevity was longer in aquatic species, in long-distance migrating species, in non-passerine birds and more marginally in closed habitats (table 1).

In the full phylogenetic model, contrasts in maximum longevity were not significantly associated with contrasts in maximum group size (β (s.e.) = -0.005 (0.007); $p = 0.51$; $r = -0.07$) or with maximum conspecific group size (β (s.e.) = -0.008 (0.007); $p = 0.25$; $r = -0.04$). In the final model, in which 47 per cent of the total variation was explained, contrasts in maximum longevity increased with contrasts for recoveries and age at first reproduction (table 1). I tested interactions between body mass and all independent variables and found that contrasts in maximum longevity increased with contrasts in body mass in non-passerine with respect to passerine species (table 1).

4. DISCUSSION

Taking into account several life-history traits and ecological variables that are known to influence maximum longevity, the results indicate that longevity is not significantly associated with group-foraging in a large sample of North American birds. Indeed, maximum foraging group size was not correlated with maximum longevity in either phylogenetically corrected or uncorrected analyses.

Previous work with more restricted datasets or with other types of sociality also hinted that group-living is not associated with longevity in birds (Møller 2006; Munshi-South & Wilkinson 2006; Blumstein & Møller 2008). Although it is possible that the true relationship between group-foraging and longevity is masked by a

confounding factor, my analysis included quite a range of likely candidates. While factors such as migration distance and habitat features appear to influence longevity in the species analysis, such factors proved unimportant in the phylogenetically corrected analysis.

It is perhaps the case that other factors associated with group-foraging may act to reduce survival and limit the scope for an increase in longevity. These factors may include increased competition for resources and increased parasite transmission in larger groups (Alexander 1974). Other factors may decrease vulnerability to predation in species that are more at risk, such as increased allocation of time to antipredator behaviour or spatio-temporal avoidance of predators (Lind & Cresswell 2005), thus again mitigating the relationship between group-foraging and longevity. A greater understanding of the relationship between predation risk and extrinsic mortality is thus needed to assess the relationship between sociality and longevity.

The comparative analysis of longevity in North American birds otherwise revealed expected and unexpected associations. For instance, in both phylogenetically corrected and uncorrected analyses, maximum longevity increased with body mass and with age at first reproduction. However, in the uncorrected analysis, non-passerine birds tended to live longer than passerine birds. In the phylogenetically corrected analysis, an increase in maximum longevity with body mass occurred in non-passerine birds. Recent work using data from captive birds suggested that maximum longevity is longer in non-passerine birds (de Magalhaes *et al.* 2007). I extend this conclusion to wild birds using a phylogenetically corrected analysis. Therefore, the results suggest that non-passerine birds gain more in longevity from a similar increase in body mass. Future work could determine if increases in body mass allow non-passerine birds the opportunity to avoid predation to a greater extent or if physiological adaptations scaling with body size operate more forcefully in non-passerine birds. Interestingly, passerine and non-passerine birds do not differ in basic metabolic rate after controlling for phylogeny and body mass (McKechnie & Wolf 2004).

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