Is sociality associated with high longevity in North American birds?

D. T. Blumstein[1,*] **and A. P. Møller**[2]

[1]*Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA*
[2]*Laboratoire de Parasitologie Evolutive, CNRS UMR 7103, Université Pierre et Marie Curie, Bâtiment A, 7ème étage, 7 quai St Bernard, Case 237, 75252 Paris Cedex 05, France*
Author for correspondence (marmots@ucla.edu).

Sociality, as a life-history trait, should be associated with high longevity because complex sociality is characterized by reproductive suppression, delayed breeding, increased care and survival, and some of these traits select for high longevity. We studied the relationship between cooperative parental care (a proxy of complex sociality) and relative maximum lifespan in 257 North American bird species. After controlling for variation in maximum lifespan explained by body mass, sampling effort, latitude, mortality rate, migration distance and age at first reproduction, we found no significant effect of cooperative care on longevity in analyses of species-specific data or phylogenetically independent standardized linear contrasts. Thus, sociality itself is not associated with high longevity. Rather, longevity is correlated with increased body size, survival rate and age of first reproduction.

Keywords: cooperative breeding; life-history theory of senescence; longevity; maximum lifespan

1. INTRODUCTION

Sociality is a life-history trait that, as a part of a syndrome of other life-history traits, should influence longevity. The logic stems from observations that more social species delay onset of reproduction, produce fewer young and have higher infant survival rates (Blumstein & Armitage 1998), and that sociality may reduce predation risk (Krause & Ruxton 2002), and therefore extrinsic mortality rate, which evolutionary models of senescence predict will influence longevity (Ricklefs 1998).

Evolutionary theories of senescence predict that longevity should be associated with extrinsic mortality (Abrams 1993). Specifically, species with high-mortality rates should have reduced maximum lifespan (e.g. Austad & Fischer 1991; Holmes & Austad 1994; Wilkinson & South 2002). Because mortality rate is, in part, the result of life-history trade-offs (theoretically, animals could allocate most of their energy to defence and none to reproduction), those that choose not to allocate energy to defence should first reproduce before those who have the luxury of a greater annual survival rate.

Body size may reduce mortality risk if larger species have fewer predators than smaller species (e.g. Werner & Gilliam 1984) and also may increase the mortality risk if large-bodied species attract predators (Wolff & Guthrie 1985; Ebensperger & Blumstein 2006). In those cases where large body size increases survival, larger species should live longer. Alternatively, increased body size may select for sociality to reduce predation risk (Ebensperger & Blumstein 2006), and the increased sociality of larger species may itself be associated with high longevity.

Perhaps more importantly, complex sociality is associated with the reproductive division of labour and emergence of social roles (Cahan *et al.* 2002). Such roles may include non-breeding helpers, which may mature into breeders, but who will have foregone direct fitness while helping. Thus, it is reasonable to quantify the relevant importance of sociality versus other factors in the evolution of high longevity.

Students of vertebrate cooperative breeding have developed the 'life-history hypothesis of cooperative breeding' which links annual survival (a factor that influences longevity) to cooperative breeding (e.g. Brown 1987; Arnold & Owens 1998; Covas & Griesser 2007). While being relevant, this hypothesis seeks to explain the evolution of cooperative breeding, not longevity, and thus important confounding variables that may influence longevity are sometimes excluded from tests.

There have been direct tests of the 'sociality–longevity hypothesis'. Keller & Genoud (1997) and Carey (2001) found relationships between sociality and longevity in insects, while Wilkinson & South (2002) included colony size in an analysis of the effects of hibernation on longevity in bats. Bat lifespan increased with hibernation, body mass and occasional cave use, but colony size had no effect on longevity. These studies did not control for some important confounding variables. Møller (2006) tested the sociality–longevity relationship with a study of European birds, using colony size as a metric of sociality. In a series of analyses that controlled for confounding variables (sampling effort, body mass, age at first reproduction and adult survival rate), he found that body mass, sampling effort and age at first reproduction had the strongest effects in the analysis based on species-specific data, while body mass and sampling effort had the strongest effects in the analysis of independent contrasts. Colony size was a weakly significant predictor in the species-specific data, but not in the analysis of independent contrasts. Further analyses revealed that this weak effect of coloniality was entirely accounted for by colonial species, on average, starting to reproduce at an older age than solitarily breeding species. Together, these results provide little support for the sociality–longevity hypothesis in vertebrates.

However, both previous vertebrate studies used colony size as a metric of sociality, and tests of the life-history hypothesis of cooperative breeding have not controlled for other important factors that may influence longevity. Coloniality, *per se*, does not address the types of relationships and social roles that should select for high longevity because while colonial animals are co-located, they may not engage in any meaningful social interactions. Moreover, recent comparative

Table 1. Pearson's product–moment correlation matrix between longevity and variables associated with longevity for 257 North American bird species (above the diagonal) and for standardized linear contrasts (below the diagonal). (Sample size for contrasts was 253 except for cooperative care, where it was 19. Values in italics are statistically significant ($p < 0.05$).)

	longevity	survival rate	body mass	no. of recoveries	latitude	migration distance	age at first reproduction	cooperative care
longevity	1.00	*0.47*	*0.65*	*0.64*	−0.03	0.01	*0.44*	−0.09
survival rate	*0.21*	1.00	*0.60*	0.00	−0.05	−0.10	*0.63*	0.02
body mass	*0.33*	*0.32*	1.00	*0.35*	0.02	−0.09	*0.53*	−0.12
no. of recoveries	*0.62*	−0.02	*0.19*	1.00	0.06	0.06	0.05	−0.06
latitude	0.03	−0.08	0.01	0.09	1.00	*0.51*	−0.07	*−0.13*
migration distance	−0.01	−0.09	*−0.14*	0.07	*0.62*	1.00	0.03	*−0.17*
age at first reproduction	*0.30*	*0.26*	*0.35*	0.06	0.00	0.03	1.00	−0.10
cooperative care	0.36	0.37	−0.14	0.08	*−0.56*	−0.02	0.35	1.00

Table 2. Relationships between longevity in birds and hypothesized explanatory variables. ($n = 257$ species and 253 contrasts. The models had the statistics $F = 78.20$, d.f. $= 7249$, $r^2 = 0.69$, $p < 0.0001$; $F = 135.30$, d.f. $= 4252$, $r^2 = 0.68$, $p < 0.0001$ and $F = 59.32$, d.f. $= 4249$, $r^2 = 0.28$, $p < 0.0001$. Effect size was Pearson's product–moment correlation coefficients.)

	sum of squares	d.f.	F	p	slope (s.e.)	effect size (Pearson's r)
full model for species						
survival rate	0.30	1	19.32	<0.0001	0.26 (0.06)	0.27
body mass	0.39	1	25.16	<0.0001	0.07 (0.01)	0.30
no. of recoveries	2.96	1	190.88	<0.0001	0.10 (0.01)	0.66
latitude	0.06	1	3.63	0.06	−0.00 (0.00)	0.12
migration distance	0.03	1	2.10	0.15	0.02 (0.02)	0.09
age at first reproduction	0.10	1	6.75	0.010	0.12 (0.05)	0.16
cooperative care	0.00	1	0.09	0.77	−0.01 (0.03)	0.02
error	3.86	249				
reduced model for species						
survival rate	0.29	1	18.53	<0.0001	0.25 (0.06)	0.26
body mass	0.37	1	23.86	<0.0001	0.07 (0.01)	0.29
no. of recoveries	3.00	1	193.24	<0.0001	0.10 (0.01)	0.66
age at first reproduction	0.15	1	9.42	0.0024	0.14 (0.05)	0.19
error	3.92	252				
reduced model for contrasts						
survival rate	0.03	1	7.97	0.005	0.15 (0.05)	0.18
body mass	0.02	1	5.41	0.021	0.06 (0.03)	0.15
no. of recoveries	0.60	1	171.34	<0.0001	0.09 (0.01)	0.64
age at first reproduction	0.03	1	7.99	0.005	0.17 (0.06)	0.18
error	0.87	249				

evidence suggests that coloniality increases predation risk, and thus decreases annual survival (Varela *et al.* 2007), which itself is associated with longevity.

We evaluated the sociality–longevity hypothesis by examining the association between cooperative parental care and longevity. Species that cooperatively breed or engage in cooperative parental care are those that have social relationships and reproductive division of labour. Cooperative parental care occurs in 612 (9%) of all species of birds and 36 (6.5%) of North American birds (Cockburn 2006). We tested the sociality–longevity hypothesis in North American birds.

2. MATERIAL AND METHODS

We obtained most data from the Patuxent Wildlife Research Center database that lists the maximum longevity record for free-living birds banded in North America, estimated to the nearest month (longevity records and number of recoveries on which these records were based). These longevity records will depend upon sampling effort because a large number of recoveries will reveal a greater longevity record. Hence, we used the number of recoveries to adjust for any bias due to sampling effort. We obtained additional data from Poole *et al.* (1993–2002) on body mass, latitude, migration

distance, adult survival rate and age at first reproduction—the variables that are known to predict longevity (Møller 2006, 2007). We obtained data on a species' cooperative breeding status from Cockburn (2006). The data are reported in the electronic supplementary material 1.

We used a phylogeny (sources reported in the electronic supplementary material 2) to calculate standardized linear contrasts (methods in the electronic supplementary material 3).

3. RESULTS

As expected, we found a significant positive relationship between longevity and adult survival rate, body mass and age at first reproduction for species-specific data and contrasts (table 1). However, after controlling for variation in longevity explained by body mass, sampling effort, latitude, mortality rate, migration distance and age at first reproduction, we found no significant effect of whether a species engaged in cooperative parental care on longevity in analyses of species-specific data or phylogenetically independent contrasts (table 2). The reduced model for contrasts only included survival rate, body mass, age at first reproduction and number of recoveries as predictors (table 2).

4. DISCUSSION

Any way examined, there was no relationship between sociality as estimated from the presence of cooperative care and maximum lifespan of free-living North American birds. Our result was not confounded by body mass, sampling effort, latitude, mortality rate, migration distance or age at first reproduction. Our independent variables were not so highly correlated that it would have been impossible to isolate the independent effect of sociality. Thus, we feel confident in concluding that sociality, itself, is not associated with increased high longevity. Because cooperative care is found in cooperative breeders, and these species exhibit those traits that should be responsible for a life-history relationship between sociality and longevity (reproductive suppression, delayed breeding, increased care and survival; Cockburn 2006), we conclude that sociality, *per se*, is unlikely to be associated with longevity. Obviously, we cannot exclude the possibility that yet another confounding variable could potentially change this conclusion, although this seems unlikely because we already included the most likely candidates. Previous studies have indicated that cooperative breeding is associated with particular habitats and life histories (Koenig *et al.* 1992; Bennett & Owens 2002), particularly annual survival (Arnold & Owens 1998), but these variables were partly controlled statistically by inclusion of latitude, body mass and annual survival in the statistical analyses.

Our results are consistent with evolutionary models of senescence. Birds that delay the onset of first reproduction, a key prediction of adaptive models of senescence (e.g. Williams 1957), live longer. Additionally, longevity is correlated with increased body size (another life-history trait) and increased annual survival rate. It is an empirical question whether increased body size works to directly reduce predation risk, or whether it works through another mechanism such as metabolic rate that scales with body size. Recent work shows that mid-sized birds suffer higher predation rates than smaller or larger species (Götmark & Post 1996; Møller & Nielsen 2006). However, these life-history traits have a relatively important effect on longevity (Møller 2006).

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