Full title:

Increased juvenile survival may not be universally linked to longevity: ecological, social and life-history drivers of age-specific mortality in birds

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Short title:

Juvenile survival-longevity relationship

Abstract

A classical prediction of the traditional evolutionary theories of ageing (tETA) is that longevity should be positively correlated with survival early on in life. However, large and unexplained variation exists in juvenile survival-longevity combinations. Here, we provide the first comparative study investigating the life-history, ecological and social correlates of juvenile survival, longevity and their combinations in 204 bird species. Overall, both measurements were positively correlated, but multiple survivals' combinations evolved, some in accordance with tETA ("positive JS-L combinations") while others contrasting it ("JS-L mismatches"). Positive JS-L combinations covaried with the pace of life proxies, whereas mismatching combinations covaried with the growing season length, where long growing seasons promoted juvenile survival, while short growing seasons promoted longevity. Interestingly, sociality explained only positive combinations, while life-history and ecological traits explained both positive and mismatching combinations. Overall, these findings challenge a main prediction of the tETA, and identify key evolutionary forces driving the coevolution between juvenile survival and longevity.

Key words:

Comparative study, ecology, evolutionary theories of ageing, first-year survival, juvenile survival, life-history evolution, maximum longevity, social system.

43 Traditional theories of aging (tETA: "mutation accumulation"[1], "antagonistic pleiotropy"[2],
44 "antagonistic pleiotropy"[3]) propose that extrinsic mortality is the main driver of longevity[4,5]. They
45 predict that higher extrinsic mortality early on in life leads to relatively few individuals reaching old
46 age, and the fitness value of prolonged lifespan is therefore small in such cases. Thus, selection to
47 extend longevity is only strong in populations with high survival early on in life (juvenile survival
48 henceforth). Accordingly, these theories predict that longevity should be positively correlated with
49 juvenile survival[2,4,6-8].

50 Although this classical prediction of tETA underlies many life-history studies, and is
51 commonly cited as being largely corroborated by existing data[9,10], support has been mixed and
52 alternative theories exist[5,11-13]. Moreover, recent theoretical and empirical studies do challenge this
53 prediction[9,14-16], and state that juvenile survival (extrinsic mortality early on in life) is not a random
54 process but does depend on age, individual condition, or population density. Accordingly, species
55 can deviate from the expected relationship between juvenile survival and longevity, by having a low
56 juvenile survival but being long-lived, or by having a high juvenile survival but being short-lived[5,9,13-
57 17]. However, it remains unclear whether these deviations represent evolved strategies modulated by
58 specific life-history, ecological and/or social factors, or whether they are pieces of a continuum of
59 randomly varying combinations.

60 Longevity is a pivotal factor shaping life-histories[18,19], but survival can vary among the stages
61 of life and differently influence the evolution of life-history traits[20-22]. Theoretical[12,23-26] and empirical
62 work on birds[27], fishes[22] and mammals[28] have highlighted the importance of considering age-specific
63 survival to understand the evolution of life-history traits. Specifically, these studies showed that age-
64 specific survival patterns that deviate from the classical prediction of tETA (e.g., low chance of
65 survival early in life but a high longevity), are linked to unusual combinations of life-history traits that
66 are characteristic to both slow- and fast-living animals[19]. For instance, turtles and crocodiles suffer
67 from high juvenile mortality, and accordingly females lay many eggs in each reproductive event (like

68 fast-living animals) despite that they are exceptionally long-lived (like slow-living animals)[29]. Thus,
69 considering the factors affecting age-specific survivals and their combination is critical to understand
70 life history evolution in general.

71 Longevity varies considerably across species. In vertebrates it ranges from a few months to
72 over 100 years[30]. Comparative work did show that adaptations that reduce extrinsic mortality,
73 including protective shells[6] or the ability to fly[31], are linked with increased longevity. Moreover, long-
74 lived species tend to be active during the period of day with the lowest predation risk[31], have a low
75 number of co-occurring predators of adults[32] or life-history traits characteristic of a slow pace of life
76 (e.g., produce few offspring, which develop slowly and mature relatively late in life)[12,18]. Additionally,
77 larger mammals and birds live longer than smaller ones[32-34].

78 In many taxa, juveniles usually have lower and more variable survival than adults[35-38]. The
79 few studies investigating juvenile survival showed that the small body size of juveniles may explain
80 their low survival in lineages with slow growth (mammals, reptiles) and indeterminate growth
81 (fish)[39,40]. In lineages with rapid body growth (birds), low juvenile survival can reflect age-dependent
82 social dominance[35] or lacking skills[41]. Besides, juvenile survival tends to be high in birds with long
83 nestling periods[42], low reproductive allocation[43,44], prolonged post-fledging care[45], or prolonged
84 association with the parents beyond independence (i.e., family-living species, see[46])[47,48] (Table 1).
85 Although a number of studies have investigated inter-specific variation in longevity[31,32,34,49,50], it is
86 unknown which factors influence survival early on in life and how this relates to longevity[51].
87 Importantly, comparative studies are lacking.

88 Here, we use phylogenetic comparative analyses to understand interspecific variation in
89 juvenile survival (measured as post-fledglings to first-year survival rate) and maximum longevity, as
90 well as their relationship, in 204 bird species. Firstly, we compare the association of (i) juvenile
91 survival and (ii) maximum longevity with life-history, ecological and social parameters. Secondly, we
92 investigate how juvenile survival and maximum longevity relate to each other, and assess which life-

93 history, ecology and social traits better explain (i) positive associations between juvenile survival and

94 longevity (i.e., as expected by the classical prediction of tETA: low-low and high-high combinations,

95 referred to as "positive JS-L combinations" henceforth), and (ii) mismatches between juvenile

96 survival and longevity (i.e., deviation from the classical prediction of tETA: low-high and high-low

97 combinations, referred to as "JS-L mismatches" henceforth).

98 Table 1| Description and prediction of the parameters investigated in this study.

	parameter's name	description	prediction	source prediction
life-history	adult body mass*	mean adult body mass (g)	larger body size confers better ability to cope with temporary food shortages, climatic fluctuations and extreme weather than smaller body size; large body size may associate with higher juvenile survival and higher longevity	39,52
	incubation period*	number of days from laying to hatching	longer incubation period may associate with higher juvenile survival and higher longevity	12,18
	nestling period*	number of days from hatching to fledging	longer nestling period may associate with higher juvenile survival and higher longevity	42
	annual parental investment*	body-mass scaled annual reproductive investment (total mass of eggs produced annually divided by adult body mass)[(a)]	higher parental investment may associate with lower juvenile survival and lower longevity	12,18,53
	chick development mode	precocial vs. non precocial; semi-altricial or semi precocial species were categorised as non precocial	precocial species should have lower juvenile survival but higher longevity because of lower parental care after hatching while the opposite is expected for altricial species	54
ecological	sedentariness	resident vs. migratory; based on the species maximum movement; sedentary species or with local movement were categorised as resident and the one with regional or inter-continental movement as migratory	costs associated with migration could translate into lower juvenile survival and lower longevity in migratory than in non-migratory species	55
	period of activity	diurnal vs. nocturnal; crepuscular species (i.e. active at dawn and dusk) were categorised as nocturnal	species that are active at night are likely to be harder for predators to detect and predators are more scarce at night thus, nocturnal species might have higher juvenile survival and live longer than diurnal species	31
	nest predation risk*	based on both most commonly used nest location and nest type; ordinally ranked: 1 = inaccessible nests in cavities, 2 = open nests in cliffs or tree, 3 = open nest in shrub-layer or the ground[(b)]	nest predation risk may alter the developmental phase of the nestling and the reproductive effort of the parents which may affect juvenile survival and longevity; greater nest predation risk may associate with lower juvenile survival and lower longevity	20
	foraging exposure*	level of exposure to predators during foraging time based on most commonly used foraging area; ordinally ranked: 1 = pelagic species, 2 = aerial foragers, 3 = terrestrial foragers	pelagic or aerial forager should have lower predation risk and be more capable of escaping from predators than species that feed on the ground; juvenile survival and longevity may be reduced in the latter more than in the formers	56,57
	vegetation cover*	cover of woody vegetation in habitat (%)	more open habitats provide less visual cover than habitats dense in vegetation, increasing the risk of being killed; thus, low vegetation density may associate with lower juvenile survival and lower longevity. The reverse may be true if vegetation	57-59

			cover, by obstructing the view of the prey, affects its survival	
	caloric content of food*	energy content of the food in kcal/100g[c]	food calory content can influence the energy available for maintenance; high calory diet may associate with higher juvenile survival and higher longevity	[60,61]
	fibre content of food*	fibre food content in g/100g[c]	food fibre content can influence digestion efficiency and thus the level of resource acquired and health; high fibre diet may associate with higher juvenile survival and higher longevity	[60,61]
	foraging cost*	level of energy demand for foraging based on most commonly used foraging technics; ordinally ranked: 1 = sit and wait hunters, 2 = swimming or short perch & short flights, 3 = aerial or under water foraging, 4 = terrestrial or gleaners [d]	species with highly energetically demanding foraging strategies may have lower juvenile survival and lower longevity than species with less energetically demanding technics	[62]
	diet specialisation	specialist (only one diet class) vs. generalist (more than one diet class)	a change in the food availability can have higher costs for specialist than generalist species as the later can deviate to other food resources; specialisation may associate with lower juvenile survival and lower longevity	[63]
	habitat specialisation	specialist (only one habitat type) vs. generalist (more than one habitat type)[e]	a change in habitat availability can have higher costs for specialist than generalist species as the latter can occupy other habitat types; specialisation is predicted to associate with lower juvenile survival and lower longevity	[64,65]
	MGS duration*	mean duration of the growing season in months[f] (i.e., month(s) of the yeuyuar in which temperature and rainfall allow significant plant productivity)	a short growing season implies changes in environmental conditions over the year, thus MGS duration can be seen as a proxy of environemental variability; less variable environments (long growing season) may associate with higher juvenile survival and longevity than highly variable environment (short growing season)	[66]
	region	breeding distribution range: northern or southern hemisphere, both hemispheres, island	southern hemisphere and island species may have higher juvenile survival and higher longevity compared to northern hemisphere species	[34,66,67]
	N avian predators*	number of sympatric adult's or independent juveniles' predator species[g]	a higher number of predators increases the risk of being predated; higher number of predators may associate with a lower juvenile survival and lower longevity	[32]
Social	parental care mode	uniparental, biparental, cooperative breeding	the presence of additional carer can reduce survival risks on young and survival costs on the other carer(s); biparental and cooperative breeding species may have higher juvenile survival and higher longevity than uniparental species	[68],but see[69,70]
	social system	family living (offspring remain at least 50 days beyond nutritional independence with parents) vs. non-family living[h]	species with prolonged post-fledging parental care or having a prolonged association with the parents beyond independence, as in family-living species, may have higher juvenile survival and lower longevity	[45,71]

Because experience (e.g., foraging, competition, reproductive strategies, anti-predation behaviours) differs between young individuals (inexperienced) and adults (experienced), we also assumed each of the abovementioned parameters to diferentially influence juvenile survival and longevity, and potentially explain variation in juvenile survival/longevity relationships.

* Included in the PCA (Table 2). The other parameters are categorical variables. (a)[56], (b)[72,73], (c)[60], (d)[74], (e)[75], (f)[76], (g)[32], (h)[46].

105 # Materials and Methods

106 **Survival data.** We collected data on juvenile survival and maximum longevity for 293 bird species
107 covering 20 taxonomic orders and 74 families (Fig. S1 in Supporting Information), using existing
108 datasets[32], the Handbook of the Birds of the World[77], the Birds of North America[78], the Handbook of
109 Australian, New Zealand and Antarctic Birds[79], the Handbook of Southern Africa[80], the Australian
110 Birds and Bats Banding Scheme database[81] and Animal Ageing and Longevity database[82] (available at
111 http://genomics.senescence.info/species/).

112 Juvenile survival was assessed as the proportion of fledglings that survive their first year of
113 life, where many juveniles die due to extrinsic mortality[83]. For species where multiple values of
114 juvenile survival were available we used their mean. Maximum longevity (maximum observed
115 lifespan) was mostly assessed with mark-recapture of ringed wild birds, but for 19 species longevity
116 was of unknown origin (captivity or wild). Earlier studies showed that longevity records in captivity
117 and the wild are highly correlated[32,34] and thus, we also included longevity data of unknown origin.
118 Longevity estimates are influenced by the sampling effort because the larger the sample the higher
119 is the chance to sample a long-lived indvidual[32]. Therefore, to adjust for any bias associated with
120 maximum longevity estimates we included the independent number of Web of Science records per
121 species (research effort) as a covariate in our analyses (available at
122 http://apps.webofknowledge.com).

123 **Life-history, ecology and social parameters.** We used a published dataset[84] that was
124 complemented with data from the sources listed above, and compiled data on life-history, ecological
125 and social parameters that may influence juvenile survival and longevity (Table 1). We could find
126 data for the 20 parameters listed in Table 1 for 204 of the 293 species (Fig. S2). Thus, 293 species
127 were considered in descriptive analyses, while a subset 204 species entered detailed phylogenetic
128 mixed models.

129 Statistical analyses. *General procedures.* All statistical analyses were performed in R version
130 3.2.2[85]. We used phylogenetic controlled mixed models in ASReml-R 3[86] to control for the
131 phylogenetic dependency among species (VSN International, Hempstead, U.K.[87]). We included
132 phylogeny as a random effect in the model in the form of a correlation matrix of distances from the
133 root of the tree to the most recent common ancestor between two species. We tested the
134 phylogenetic effect with a likelihood ratio test where 2 times the difference in log-likelihood
135 between the model with and without the phylogeny is tested against a χ^2 distribution with one
136 degree of freedom[88]. To account for phylogenetic uncertainty, all ASReml-R models were run with
137 300 different phylogenetic trees obtained from www.birdtree.org[89]. We averaged the estimates
138 from the 300 models and present the averaged estimates and the Fs_{300} (proportion of trees for
139 which the p-value associated with an estimate was <0.05). Individual p-values were obtained
140 through a conditional Wald F-test. All continuous variables were standardised by centring (around
141 the mean) and scaling (by the standard deviation) them, to allow direct comparison of the model
142 estimates[90], but we present raw data in the figures. We checked for the assumptions of normally
143 distributed and homogeneous residuals by visually inspecting histograms and qq-plots of the
144 residuals as well as residuals plotted against fitted values.

145 To reduce the multidimensionality of our predictor variables and to reduce their
146 collinearity[91], we performed a principal component analysis (PCA) with varimax rotation including all
147 12 continuous predictors, and extracted 7 PC's given in Table 2. Prior to the PCA, the distribution of
148 these predictors was checked graphically and, if necessary, transformed to obtain a more
149 symmetrical distribution, and then standardised (see above).

Table 2 | Results of the Principal Component Analysis (PCA) with varimax rotation on the 12 continuous predictors.

				life-history pace	**exposure to predators**	**food fibre**	**nest predation risk**	**N avian predators**	**foraging cost**	**MGS duration**	
category	transformation	variable	nº component	1	7	2	6	3	5	4	h2
life-history	ln	adult body mass		**0.90**	-0.25	-0.08	0.13	-0.01	-0.17	-0.12	0.95
	none	annual parental investment		**-0.89**	0.14	-0.17	0.13	0.14	-0.05	-0.02	0.87
	sqrt	incubation period		**0.76**	-0.35	0.23	-0.03	-0.10	-0.28	-0.04	0.84
	none	nestling period		0.51	0.04	0.44	-0.58	-0.13	0.01	0.20	0.85
ecological	none	nest predation risk		0.05	-0.10	-0.12	**0.94**	-0.12	0.09	-0.07	0.93
	none	foraging cost		-0.17	0.02	-0.11	0.08	-0.07	**0.96**	-0.05	0.98
	none	calorie content of food		0.15	0.49	0.62	0.02	0.44	0.01	-0.01	0.83
	ln	fibre content of food		-0.11	0.16	**-0.89**	0.22	-0.01	0.15	-0.10	0.92
	none	foraging exposure		-0.30	**0.86**	-0.04	-0.01	0.04	-0.02	0.00	0.83
	sqrt	vegetation cover		-0.21	**0.85**	-0.01	-0.13	-0.08	0.05	0.11	0.80
	sqrt	N avian predators		-0.18	-0.03	0.08	-0.07	**0.95**	-0.05	0.00	0.95
	none	MGS duration		-0.06	0.08	0.08	-0.11	-0.01	-0.05	**0.98**	0.99
		SS loadings		2.68	1.94	1.5	1.34	1.15	1.07	1.05	
		cumulative variance explained (%)		22	39	51	62	72	81	89	

We considered coefficients of correlation greater than 0.7 or less than -0.7 to be high loadings (highlighted in bold). h2 is the communality of the 7 components. ln: natural logarithm, sqrt : Square root

153 Full mixed models included the 7 PC's (Table 2), the 8 categorical variables described in Table
154 1, and as covariates research effort (log transformed) and body mass (log transformed) to control for
155 allometry[32,49]. Since the life-history pace PC was loaded by adult body mass (Table 2) and therefore
156 partially controlling for allometry, we only included the residuals from a linear model between the
157 natural logarithm of adult body mass and the life-history pace component as body-mass covariate.
158 This way the presence in the model of both the life-history pace PC and the residual body mass
159 allows to fully control for allometry.

160 The importance of first-year survival for fitness benefits is likely to depend on the age at first
161 reproduction (AFR) (63.8% of the species had an AFR ≤ 1 year old, 17%]1; 2], 9.6%]2; 3] and 9.6% >
162 3 years old, Fig. S3). Therefore, we re-ran the PCA and all the following analyses on a subset of
163 species for which AFR was available (N=188, Fig. S4). PCA output remained the same, and AFR
164 loaded positively on the life-history pace PC (Table S1). The linear mixed-effects models gave
165 qualitatively similar output (Tables S2, S3, S4) suggesting that in our set of species it is unlikely that
166 AFR affected our analyses, and thus we present in the manuscript the analyses including all species
167 (N=204).

168 *Correlates of juvenile survival and longevity.* We ran two phylogenetically controlled linear mixed-
169 effects models including the same life-history, ecological and social predictors to assess the factors
170 correlating with juvenile survival and with longevity. We fitted in both cases the full models (i.e., no
171 model selection applied) to obtain comparable estimates of the same set of predictors in both
172 models. To compare the influence of each predictor on both response variables, juvenile survival and
173 longevity were standardised[90].

174 *Combinations of juvenile survival and longevity.* The second set of analyses assessed factors that
175 were associated with combinations of juvenile survival and longevity that (i) concurred with (positive
176 JS-L combinations) or (ii) deviated from (JS-L mismatches) the positive correlation between juvenile
177 survival and longevity, predicted by tETA. We captured the natural patterns of association between

178 juvenile survival rate and maximum longevity using a PCA approach on the two log-transformed and
179 standardised survival variables. The PCA resulted in two principal components (PCs, Table S5). Due
180 to the properties of a PC data rotation, PC1 was loaded positively by both survival estimates (Table
181 S5). Thus, it describes a tied link between juvenile survival and longevity, capturing patterns that
182 concur with the classical prediction of tETA (cases positioned on PC1 represent the most typical
183 cases of positive JS-L combinations). PC2 was loaded positively by juvenile survival rate and
184 negatively by maximum longevity (Table S5). Being perpendicular to PC1, it captures how much a
185 species deviates from the overall expected association, and thus, how much it deviates from the
186 classical prediction of tETA (JS-L mismatches).

187 We ran two separate phylogenetically controlled linear mixed-effects models to assess the
188 factor associated with absolute values of (i) PC1 (positive JS-L combinations) and (ii) PC2 (JS-L
189 mismatches). We included the same set of predictors and covariates as in the full models of juvenile
190 survival and longevity analyses, and included the sign (positive or negative) of the corresponding PC
191 as a factor and in interaction with each predictor. The latter allowed us to assess the correlates of
192 each possible combination of juvenile survival and longevity, i.e., to investigate how species
193 attributes associated with (i) high juvenile survival-high longevity vs. low juvenile survival-low
194 longevity combinations (positive JS-L combinations, analysis of PC1), and (ii) deviation towards
195 higher juvenile survival-lower longevity vs. lower juvenile survival-higher longevity (JS-L mismatches,
196 analysis of PC2). For both models, we used a backward model selection process. We successively
197 removed terms with $p > 0.10$, starting with the highest-order interactions and following with the
198 simple effects. We compared models including and excluding the focal predictor using *model.sel*
199 function from the MuMIn package[92]. The decision to exclude the predictor was based on the AICc
200 criterion using a ΔAICc (i.e., $AICc_{included} – AICc_{excluded}$) > 2 as threshold[93]. Results of the full models are
201 provided in Table S6 and S7.

202

203 Table 3 | Correlates of juvenile survival and longevity. Results from phylogenetically controlled linear
204 mixed-effect models testing the influence of key life-history, ecological and social traits on juvenile
205 survival and longevity, respectively.

		juvenile survival (first-year survival rate)		**longevity** (maximum longevity)	
		estimates*	Fs_{300}	estimates*	Fs_{300}
(intercept)		0.20	0.02	**-0.70**	**1**
residual adult body mass (covariate)		-0.02	0	0.03	0
ln (research effort) (covariate)		**-0.14**	**1**	**0.18**	**1**
life-history pace PC		**0.50**	**1**	**0.42**	**1**
nest predation risk PC		**0.19**	**0.92**	-0.10	0
exposure to predators PC		-0.17	0	**-0.22**	**0.88**
N avian predators PC		0.07	0	-0.05	0
MGS duration PC		-0.01	0	-0.08	0
foraging cost PC		-0.14	0	-0.06	0
food fibre PC		-0.13	0	0.03	0
diet specialisation	generalist	0.00	0	0.00	0
	specialist	0.04		-0.07	
habitat specialisation	generalist	0.00	0	0.00	0
	specialist	0.10		-0.11	
period of activity	diurnal	0.00	0	0.00	0
	nocturnal	0.31		-0.38	
sedentariness	resident	0.00	0	0.00	0
	migratory	0.14		0.07	
region	both	0.00	0	0.00	0
	island	-0.32		-0.12	
	northern	0.39		-0.16	
	southern	0.35		-0.21	
chick development mode	non-precocial	0.00	0	0.00	0
	precocial	-0.10		-0.36	
parental care mode	biparental	0.00	0	0.00	0
	cooperation	-0.08		-0.17	
	uniparental	0.53		0.34	
social system	family-living	0.00	0	0.00	0
	non family-living	-0.23		-0.25	

206 **Bold** estimates correspond to predictors with significant effect.
207 PC: principal component from Table 2.
208 Fs_{300}: frequency of trees for which p-values < 0.05.
209 *: reference level of categorical variables have an estimate of 0; estimates reflect difference in slope
210 between the reference level and focal level.
211 Phylogenetic effect longevity model: likelihood ratio test: LRT = 29.52, df = 1, p < 0.001
212 Phylogenetic effect juvenile survival model: likelihood ratio test: LRT = 3.33, df = 1, p = 0.0

Results

Correlates of juvenile survival and longevity. Juvenile survival rate ranged from 0.08 to 0.95 (0.39 ± 0.16; mean ± SD) and maximum longevity ranged from 5 to 51 (17.7 ± 9.0) years. Juvenile survival and longevity both correlated with the life-history pace PC, where species with a slow life-history pace (large body size, low annual reproductive investment, long incubation period; Table 1) had significantly higher juvenile survival and greater longevity compared to species with a fast life-history pace (small body size, high annual reproductive investment, short incubation period; Tables 1 and 3). Moreover, juvenile survival was higher in species with a high nest predation risk (open nest close to the ground or on the ground; Tables 1 and 3), while longevity was greater in species with a low exposure of adults to predators (pelagic forager, living in open habitat; Tables 1 and 3). The phylogenetic effect was only significant for longevity (Table 3).

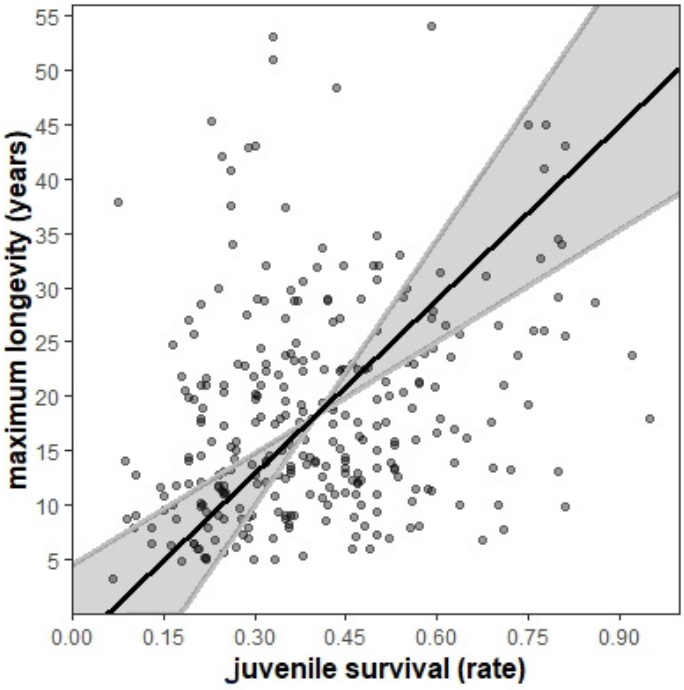

Figure 1 | Correlation between juvenile survival (first-year survival) and maximum longevity on 293 bird species.
RMA slope = 53.15, 95% CI (34.13, 81.71); $r_{Spearman}$ = 0.28, S = 3003600, p <0.0001. 64 species (22%) are inside and 229 (78%) outside the 95%CI of the regression line (shaded area). See Fig. S6 for species identification.

230 Combinations of juvenile survival and longevity. Juvenile survival and longevity were positively
231 correlated ($r_{Spearman}$= 0.28, p <0.0001) (Figs. 1 and S5) and the slope of their linear regression was
232 significant (N = 293, RMA slope = 53.15, 95% CI of the slope: 34.13, 81.71, p < 0.0001). However,
233 there were major deviations from the regression line (R^2 = 0.07), and 229 of 293 species (78%) fell
234 outside the 95% confidence interval (CI) of the RMA regression (Figs. 1 and S6). We note that the
235 percentage of species that deviate from the overall juvenile survival-longevity relationship was only
236 a slightly lower (71%) when using a more conservative CI (99%CI: Fig. S7).

237 *Positive associations between juvenile survival and longevity.* In general, positive JS-L
238 combinations were associated with family living, or a high risk of nest predation (open nest on or
239 close to the ground, Table 1) but those effects were independent of the direction of the relationship
240 (significant simple effects: Table S8). Opposite positive combinations of juvenile survival and
241 longevity (low-low vs. high-high) were differently associated with specific-species attributes. This
242 was reflected by the significant two-way interactions between the sign of PC1 (negative: low-low vs.
243 positive: high-high JS-L combinations, Fig. 2) and sedentariness, exposure to predators, life-history
244 pace and parental care mode. Species with high juvenile survival-high longevity combinations were
245 migratory, had a low exposure to adult predators (pelagic forager, living in open habitat; Table 1), a
246 slow life-history pace or uniparental care. In contrast, species with low juvenile survival-low
247 longevity combinations were sedentary, had high exposure to predators, a fast life-history pace, or
248 had bi-parental or cooperative offspring care) (Figs. 2 and S8, Table S8).

249 *Mismatches between juvenile survival and longevity.* In general, JS-L mismatches were associated
250 with low exposure to adult predators (pelagic foraging, living in open habitat, Table 1) or being a
251 habitat generalist, but these effects were independent of the direction of the relationship between
252 juvenile survival and longevity (significant simple effects: Table S9). Opposite JS-L mismatches (low-
253 high vs. high-low) were differently associated with specific-species attributes as reflected by the
254 significant two-way interactions between the sign of PC2 (negative: low-high vs. positive: high-low

JS-L combinations, Fig. 2) and period of activity, MGS duration and life-history pace. Species with stronger than expected combinations of high juvenile survival-low longevity lived in stable environments with long growing seasons (Table 1), or were nocturnal. In contrast, species with outstandingly low juvenile survival-high longevity combinations lived in variable environment with short growing seasons (Table 1) or had a slow life-history pace (Figs. 2 and S9, Table S9).

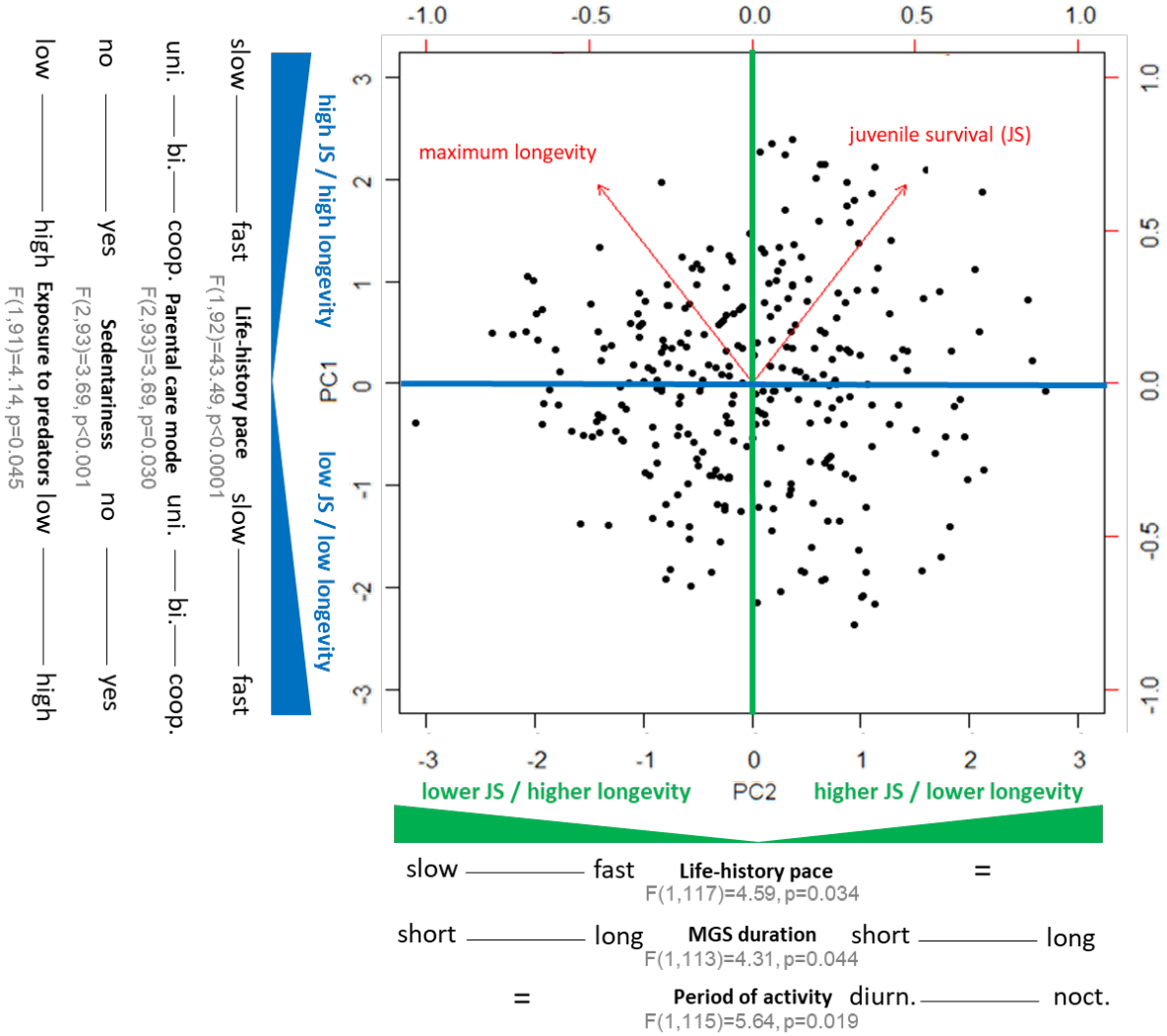

Figure 2 | Correlates of the positive (PC1) and mismatching (PC2) combinations of juvenile survival and longevity. Graphical summary of the main results from the backward model selections on phylogenetically controlled linear mixed models investigating which life-history, ecological and social traits characterised species with different combinations of juvenile survival (first-year survival) and longevity (N=204).
The blue axis (PC1) represents combinations that concur with tETA's classical prediction (high juvenile survival associated with high longevity or vice versa). The green axis (PC2) represents combinations that deviate from tETA's classical prediction (deviation towards higher juvenile survival associated with lower longevity or vice versa). Graphics of each independent results are provided in Figs. S8 and S9. See Fig. S10 for species identification and Fig. S11 for order identification.
JS = juvenile survival, Coop. = cooperative breeding, bi. = biparental care, uni. = uniparental care, noct. = nocturnal, diurn. = diurnal, F(…,...) = Conditional F statistic and its degrees of freedoms averaged over the 300 models, p = averaged p value over the 300 models.

Discussion

Empirical studies often use longevity as a proxy of life-history pace, based on the assumption of tETA that juvenile survival and longevity are positively correlated[2,8,12,94]. While this pattern is supported by previous work[2,6,7,12] and is generally visible in our data, our analyses show that around 70% of bird species significantly deviate from this overall juvenile survival-longevity positive relationship (Figs. 1 and S6). Our analyses demonstrate that a wide range of survivals' combinations evolved, some in accordance with the classical prediction of tETA while others contrasting it, partly supporting recent developments in this field[9,14-16]. Overall, this study raises awareness on the fact that the relationship between juvenile survival and longevity is not a black or white concept, but a range of grey nuances, and identifies key evolutionary forces driving the coevolution between juvenile survival and longevity.

Correlates of juvenile survival and longevity. On average, a slow life-history pace (in our study corresponding to: large body size, low annual reproductive investment, long incubation period, Table 2) is associated with high juvenile survival and longevity (Table 3), supporting life-history theory[12,19]. However, while juvenile survival and longevity are positively correlated (Figs. 1 and S5), their individual variation are also associated with particular parameters (Table 3; [95]), supporting findings from mammals[21]. Our analyses show that nest predation risk (index based on nest location and nest type, Table 1) only influences juvenile survival while exposure to predators of adults (index of habitat openness, Table 1 and 2) only influences longevity (Table 3). Consequently, these factors are likely to play an important role in the evolution of diverse juvenile survival-longevity patterns.

Juveniles are often less conspicuous than adults due to more cryptic coloration and behaviours[96-99], reducing their vulnerability to predation. Accordingly, a high exposure to predators of adults is associated with decreased longevity only (Table 3). In contrast, a low nest predation risk is associated with low juvenile survival only (Table 3). In this study, this latter association concerns mainly cavity-breeding species (Table 2) known to often experience a lower nest predation risk than

298 open-nesting species[72]. However, in cavities, nestlings are often exposed to ectoparasites[100,101],
299 reducing their body condition[100,102,103], potentially explaining a reduced juvenile survival in these
300 species[95] (Table 3). Therefore, nesting habits that provide short-term benefits early on in life may
301 have negative down-streams effect on juvenile survival that so far were not anticipated (but see[42]).

302 Combinations of juvenile survival and longevity. Most species (78%) deviate significantly from the
303 positive juvenile survival-longevity regression revealing the existence of a continuum of patterns
304 (Figs. 1 and S6), challenging the classical assumption of tETA[2,6,7,12]. The degree of this deviation varies
305 considerably between species (Figs. 2 and S10), demonstrating that the association between juvenile
306 survival and longevity evolved towards multiple adaptive combinations in birds. Some part of this
307 mismatch may represent random variation and cannot be explained by consistent biological
308 patterns. However, variation in survival at different life stages is likely to represent distinct
309 strategies, shaped by natural selection to achieve the most optimal solutions in a given combination
310 of external and internal factors. Thus, instead of forcing the long-accepted pattern of tETA or
311 challenging it with opposing hypotheses, we should adopt a more diverse approach. Accordingly,
312 one should embrace that various possible juvenile survival-longevity combinations exist (including
313 the non-tETA compliant ones), and their actual values should be assumed to maximize population
314 viability. Our framework integrating ecological, life-history and social moderators clearly
315 demonstrates that such a heterogeneous picture is biologically more realistic.

316 Our analyses on the associations between juvenile survival and longevity do not allow us to
317 investigate unusual juvenile survival and longevity separately, limiting our ability to identify
318 underlying mechanisms. This would require an in-depth view of what is happening between
319 individuals, calling for more comparative studies and experiments on both juvenile survival and
320 longevity at the intra-species level. However, species-level deviations from the positive correlation
321 between juvenile survival and longevity likely reflect that certain selective factors only influence
322 specific life stages[35,104]. Patterns observed between different taxa can be thought of as averaged

323 outcomes of selective pressures, acting over long periods of time. Indeed, age-dependent changes in
324 body size, coloration, behaviour, or the onset of reproduction and senescence, can affect extrinsic
325 and intrinsic mortality differently at different life stages[35,104]. For example, juveniles early on in life
326 are often smaller than adults, making them more susceptible to predation[32,39]. Also, juvenile survival
327 may be low in species that live in challenging environments, have elaborate foraging techniques or a
328 specialised diet, as juveniles in those species seem to need more time to acquire adult skill
329 levels[62,68,105]. In contrast, only adults pay costs of reproduction, which may reduce their longevity
330 directly, or indirectly, for instance through increased exposure to predators as a consequence of
331 increased foraging effort[106], or displaying the own quality to potential partners[107].

332 *Positive associations between juvenile survival and longevity.* Positive JS-L combinations are in
333 accordance with the classical prediction of tETA, indicating that life-history, ecological, and social
334 parameters have similar effects on juvenile survival and longevity. Our analyses show that high
335 juvenile survival-high longevity combinations are found in species that are migratory, have a low
336 exposure to predators, a slow life-history pace or uniparental care (Fig. 2), and are mostly observed
337 in Accipitriformes, Anseriformes, Charadriiformes, and Pelicaniformes (Fig. S11). In contrast, low
338 juvenile survival-low longevity combinations are found in species that are sedentary, have a high
339 exposure to predators, a fast life-history pace, or have cooperative or biparental brood care (Fig. 2),
340 and are mostly observed in Galliformes and Passeriformes (Fig. S11).

341 Migration is regularly found in species breeding at higher latitudes or altitudes, allowing
342 them to escape harsh winter conditions[55]. In most of these species, juveniles and adults are
343 migratory, thus affecting both life stages. While previous research showed that migration can be
344 costly (i.e., being associated with smaller relative brain sizes;[108]), our results highlight that it has a
345 positive effect on survival in general. Moreover, a low exposure to predators is beneficial for both
346 juvenile and adults, making pelagic species particularly long-lived[32]. As predicted by life-history
347 theory, species with a slow life-history pace have increased juvenile survival and longevity[12,19,66].

348 Furthermore, parental care is costly[54,109]. To ensure the survival of their offspring, parents provide
349 them with food, thermoregulation, and protection from predators, which, on top of being energy
350 demanding, exposes the parents to an increased risk of predation[54,110]. Thus, it seems surprising that
351 species with uniparental care have combination of higher juvenile survival and longevity compared
352 to biparental and cooperatively breeding species. A possible explanation is that particularly species
353 with low costs of parental care evolved uniparental care, leading to increased juvenile survival and
354 longevity. Clearly, this finding calls for further studies to investigate both the drivers and
355 consequences of uniparental care.

356 *Mismatches between juvenile survival and longevity.* Mismatching combinations of juvenile
357 survival and longevity suggest that certain factors specifically act upon juvenile survival or longevity,
358 or have opposing effects on juvenile survival and longevity, leading to age-specific differences in
359 survival. Our results demonstrate that high juvenile survival-low longevity combinations are found in
360 species that live in stable environments with long growing seasons or are nocturnal (Fig. 2), and are
361 mostly observed in Apodiformes and Galliformes (Fig. S11). In contrast, low juvenile survival-high
362 longevity combinations are found in species that live in variable environments with short growing
363 seasons or have a slow life-history pace (Fig. 2), and are mostly observed in Pelicaniformes and
364 Procellariiformes (Fig. S11).

365 Conceivably, living in stable environments may particularly affect juvenile survival, reducing
366 their winter mortality, while the opposite is the case in variable environments. The high juvenile
367 survival-low longevity combinations found in nocturnal or crepuscular species is likely to reflect
368 reduced juvenile mortality, given that most predators of birds are diurnal bird species[32]. In contrast,
369 combinations of low juvenile survival-high longevity found in species with a slow life-history pace is
370 likely to reflect that long-lived species particularly invest in longevity, at the expense of high juvenile
371 survival in some species. Generally, interpreting those interactions is not straightforward. We urge

372 further studies, especially longitudinal ones, to improve our understanding of the interesting
373 interspecific patterns revealed here.

374 Conclusions. Our comparative study provides novel insights into interspecific variation in juvenile
375 survival, longevity and their combination in birds, and highlights the importance to consider age-
376 specific survival to understand the evolution of life-history traits[22,25,26,42,111]. It increases our
377 knowledge on the correlates of longevity and the under-studied juvenile survival and shows that
378 most species deviate from the classical prediction of tETA. Our findings show that multiple adaptive
379 combinations of juvenile survival and longevity evolved (more than commonly expected), some in
380 accordance with tETA's classical prediction while others contradict it. Accordingly, we call for a
381 novel, more diverse, approach to understand the link between juvenile survival and longevity, and to
382 move beyond the classical prediction of tETA. Our analyses demonstrate that positive JS-L
383 combinations co-vary along the pace of life continuum, and JS-L mismatches co-vary with the length
384 of the growing season, where long growing seasons promote juvenile survival, while short growing
385 seasons promote longevity. Interestingly, sociality (parental care) only explains positive JS-L
386 combinations, while ecological and life-history traits explain both positive JS-L combinations
387 (sedentariness, exposure to predators, pace of life) and JS-L mismatches (length of growing season,
388 period of activity, pace of life). Finally, our analysis emphasizes the need of not only studying typical
389 patterns, predicted by accepted hypotheses – but also looking at outlying cases, that may embody
390 genuine biological patterns rather than random deviations from assumed relationships.

391 Overall, this study reveals that the various combinations of juvenile survival and longevity
392 observed are shaped by a distinct and limited set of species-specific life-history, ecological and social
393 attributes. This may reflect divergent selection on each survival estimate, or that divergent age-
394 specific survival is at the origin of diversity in species attributes[112]. Finally, species with unexpected
395 age-specific survival relationships are more likely to evolve uncommon combination of life-history

traits[28]. Thus, insights into key factors associating with unusual age-specific survival (such as the one found in this study) could contribute to a better understanding of life-history evolution[22,25-28,42,111].

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Authorship:

M.G. and E.M. compiled part of the data, E.M. performed all statistical analyses and wrote the first draft of the manuscript. M.G. and S.M.D contributed suggestions and text to subsequent drafts. S.M.D helped with the statistical methods. All authors contributed to revisions and gave final approval for publication.

Competing Interests statement:

The research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data accessibility:

The datasets supporting this article have been uploaded as part of the Supporting Information and will be archived in Dryad. The data DOI will be included at the end of the article.

Figure Legend:

Figure 1: Correlation between juvenile survival (first-year survival) and maximum longevity on 293 species.

Figure 2: Graphical summary of the key results from the backward model selections on phylogenetically controlled linear mixed models investigating which life-history, ecological and social traits characterised species with different combinations of juvenile survival (first-year survival) and longevity.

Table Legend:

Table 1. Description and prediction of the parameters investigated in this study.

Table 2. Results of the Principal Component Analysis (PCA) with varimax rotation on the 12 continuous predictors.

Table 3. Results from phylogenetically controlled linear mixed-effect models testing the influence of key life-history, ecological and social traits on juvenile survival and longevity, respectively.

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Tables:

Table 1| Description and prediction of the parameters investigated in this study.

	parameter's name	description	prediction	source prediction
life-history	adult body mass*	mean adult body mass (g)	larger body size confers better ability to cope with temporary food shortages, climatic fluctuations and extreme weather than smaller body size; large body size may associate with higher juvenile survival and higher longevity	39,52
	incubation period*	number of days from laying to hatching	longer incubation period may associate with higher juvenile survival and higher longevity	12,18
	nestling period*	number of days from hatching to fledging	longer nestling period may associate with higher juvenile survival and higher longevity	42
	annual parental investment*	body-mass scaled annual reproductive investment (total mass of eggs produced annually divided by adult body mass)[(a)]	higher parental investment may associate with lower juvenile survival and lower longevity	12,18,53
	chick development mode	precocial vs. non precocial; semi-altricial or semi precocial species were categorised as non precocial	precocial species should have lower juvenile survival but higher longevity because of lower parental care after hatching while the opposite is expected for altricial species	54
ecological	sedentariness	resident vs. migratory; based on the species maximum movement; sedentary species or with local movement were categorised as resident and the one with regional or inter-continental movement as migratory	costs associated with migration could translate into lower juvenile survival and lower longevity in migratory than in non-migratory species	55
	period of activity	diurnal vs. nocturnal; crepuscular species (i.e. active at dawn and dusk) were categorised as nocturnal	species that are active at night are likely to be harder for predators to detect and predators are more scarce at night thus, nocturnal species might have higher juvenile survival and live longer than diurnal species	31
	nest predation risk*	based on both most commonly used nest location and nest type; ordinally ranked: 1 = inaccessible nests in cavities, 2 = open nests in cliffs or tree, 3 = open nest in shrub-layer or the ground[(b)]	nest predation risk may alter the developmental phase of the nestling and the reproductive effort of the parents which may affect juvenile survival and longevity; greater nest predation risk may associate with lower juvenile survival and lower longevity	20
	foraging exposure*	level of exposure to predators during foraging time based on most commonly used foraging area; ordinally ranked: 1 = pelagic species, 2 = aerial foragers, 3 = terrestrial foragers	pelagic or aerial forager should have lower predation risk and be more capable of escaping from predators than species that feed on the ground; juvenile survival and longevity may be reduced in the latter more than in the formers	56,57
	vegetation cover*	cover of woody vegetation in habitat (%)	more open habitats provide less visual cover than habitats dense in vegetation, increasing the risk of being killed; thus, low vegetation density may associate with lower juvenile survival and lower longevity. The reverse may be true if vegetation cover, by obstructing the view of the prey, affects its survival	57-59
	caloric content of food*	energy content of the food in kcal/100g[(c)]	food calory content can influence the energy available for maintenance; high calory diet may associate with higher juvenile survival and higher longevity	60,61

	fibre content of food*	fibre food content in g/100g[c]	food fibre content can influence digestion efficiency and thus the level of resource acquired and health; high fibre diet may associate with higher juvenile survival and higher longevity	60,61
	foraging cost*	level of energy demand for foraging based on most commonly used foraging technics; ordinally ranked: 1 = sit and wait hunters, 2 = swimming or short perch & short flights, 3 = aerial or under water foraging, 4 = terrestrial or gleaners [d]	species with highly energetically demanding foraging strategies may have lower juvenile survival and lower longevity than species with less energetically demanding technics	62
	diet specialisation	specialist (only one diet class) vs. generalist (more than one diet class)	a change in the food availability can have higher costs for specialist than generalist species as the later can deviate to other food resources; specialisation may associate with lower juvenile survival and lower longevity	63
	habitat specialisation	specialist (only one habitat type) vs. generalist (more than one habitat type)[e]	a change in habitat availability can have higher costs for specialist than generalist species as the latter can occupy other habitat types; specialisation is predicted to associate with lower juvenile survival and lower longevity	64,65
	MGS duration*	mean duration of the growing season in months[f] (i.e., month(s) of the yeuyuar in which temperature and rainfall allow significant plant productivity)	a short growing season implies changes in environmental conditions over the year, thus MGS duration can be seen as a proxy of environemental variability; less variable environments (long growing season) may associate with higher juvenile survival and longevity than highly variable environment (short growing season)	66
	region	breeding distribution range: northern or southern hemisphere, both hemispheres, island	southern hemisphere and island species may have higher juvenile survival and higher longevity compared to northern hemisphere species	34,66,67
	N avian predators*	number of sympatric adult's or independent juveniles' predator species[g]	a higher number of predators increases the risk of being predated; higher number of predators may associate with a lower juvenile survival and lower longevity	32
Social	parental care mode	uniparental, biparental, cooperative breeding	the presence of additional carer can reduce survival risks on young and survival costs on the other carer(s); biparental and cooperative breeding species may have higher juvenile survival and higher longevity than uniparental species	68,but see69,70
	social system	family living (offspring remain at least 50 days beyond nutritional independence with parents) vs. non-family living[h]	species with prolonged post-fledging parental care or having a prolonged association with the parents beyond independence, as in family-living species, may have higher juvenile survival and lower longevity	45,71

Because experience (e.g., foraging, competition, reproductive strategies, anti-predation behaviours) differs between young individuals (inexperienced) and adults (experienced), we also assumed each of the abovementioned parameters to diferentially influence juvenile survival and longevity, and potentially explain variation in juvenile survival/longevity relationships.

* Included in the PCA (Table 2). The other parameters are categorical variables. (a)[56], (b)[72,73], (c)[60], (d)[74], (e)[75], (f)[76], (g)[32], (h)[46].

Table 2 | Results of the Principal Component Analysis (PCA) with varimax rotation on the 12 continuous predictors.

				life-history pace	**exposure to predators**	**food fibre**	**nest predation risk**	**N avian predators**	**foraging cost**	**MGS duration**	
category	transformation	variable	nº component	1	7	2	6	3	5	4	h2
life-history	ln	adult body mass		**0.90**	-0.25	-0.08	0.13	-0.01	-0.17	-0.12	0.95
	none	annual parental investment		**-0.89**	0.14	-0.17	0.13	0.14	-0.05	-0.02	0.87
	sqrt	incubation period		**0.76**	-0.35	0.23	-0.03	-0.10	-0.28	-0.04	0.84
	none	nestling period		0.51	0.04	0.44	-0.58	-0.13	0.01	0.20	0.85
ecological	none	nest predation risk		0.05	-0.10	-0.12	**0.94**	-0.12	0.09	-0.07	0.93
	none	foraging cost		-0.17	0.02	-0.11	0.08	-0.07	**0.96**	-0.05	0.98
	none	calorie content of food		0.15	0.49	0.62	0.02	0.44	0.01	-0.01	0.83
	ln	fibre content of food		-0.11	0.16	**-0.89**	0.22	-0.01	0.15	-0.10	0.92
	none	foraging exposure		-0.30	**0.86**	-0.04	-0.01	0.04	-0.02	0.00	0.83
	sqrt	vegetation cover		-0.21	**0.85**	-0.01	-0.13	-0.08	0.05	0.11	0.80
	sqrt	N avian predators		-0.18	-0.03	0.08	-0.07	**0.95**	-0.05	0.00	0.95
	none	MGS duration		-0.06	0.08	0.08	-0.11	-0.01	-0.05	**0.98**	0.99
		SS loadings		2.68	1.94	1.5	1.34	1.15	1.07	1.05	
		cumulative variance explained (%)		22	39	51	62	72	81	89	

We considered coefficients of correlation greater than 0.7 or less than -0.7 to be high loadings (highlighted in bold). h2 is the communality of the 7 components. ln: natural logarithm, sqrt : Square root

Table 3 | Correlates of juvenile survival and longevity. Results from phylogenetically controlled linear mixed-effect models testing the influence of key life-history, ecological and social traits on juvenile survival and longevity, respectively.

		juvenile survival (first-year survival rate)		**longevity** (maximum longevity)	
		estimates*	Fs_{300}	estimates*	Fs_{300}
(intercept)		0.20	0.02	**-0.70**	**1**
residual adult body mass (covariate)		-0.02	0	0.03	0
ln (research effort) (covariate)		**-0.14**	**1**	**0.18**	**1**
life-history pace PC		**0.50**	**1**	**0.42**	**1**
nest predation risk PC		**0.19**	**0.92**	-0.10	0
exposure to predators PC		-0.17	0	**-0.22**	**0.88**
N avian predators PC		0.07	0	-0.05	0
MGS duration PC		-0.01	0	-0.08	0
foraging cost PC		-0.14	0	-0.06	0
food fibre PC		-0.13	0	0.03	0
diet specialisation	generalist	0.00	0	0.00	0
	specialist	0.04		-0.07	
habitat specialisation	generalist	0.00	0	0.00	0
	specialist	0.10		-0.11	
period of activity	diurnal	0.00	0	0.00	0
	nocturnal	0.31		-0.38	
sedentariness	resident	0.00	0	0.00	0
	migratory	0.14		0.07	
region	both	0.00	0	0.00	0
	island	-0.32		-0.12	
	northern	0.39		-0.16	
	southern	0.35		-0.21	
chick development mode	non-precocial	0.00	0	0.00	0
	precocial	-0.10		-0.36	
parental care mode	biparental	0.00	0	0.00	0
	cooperation	-0.08		-0.17	
	uniparental	0.53		0.34	
social system	family-living	0.00	0	0.00	0
	non family-living	-0.23		-0.25	

Bold estimates correspond to predictors with significant effect.
PC: principal component from Table 2.
Fs_{300}: frequency of trees for which p-values < 0.05.
*: reference level of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.
Phylogenetic effect longevity model: likelihood ratio test: LRT = 29.52, df = 1, $p < 0.001$
Phylogenetic effect juvenile survival model: likelihood ratio test: LRT = 3.33, df = 1, $p = 0.07$

Figures:

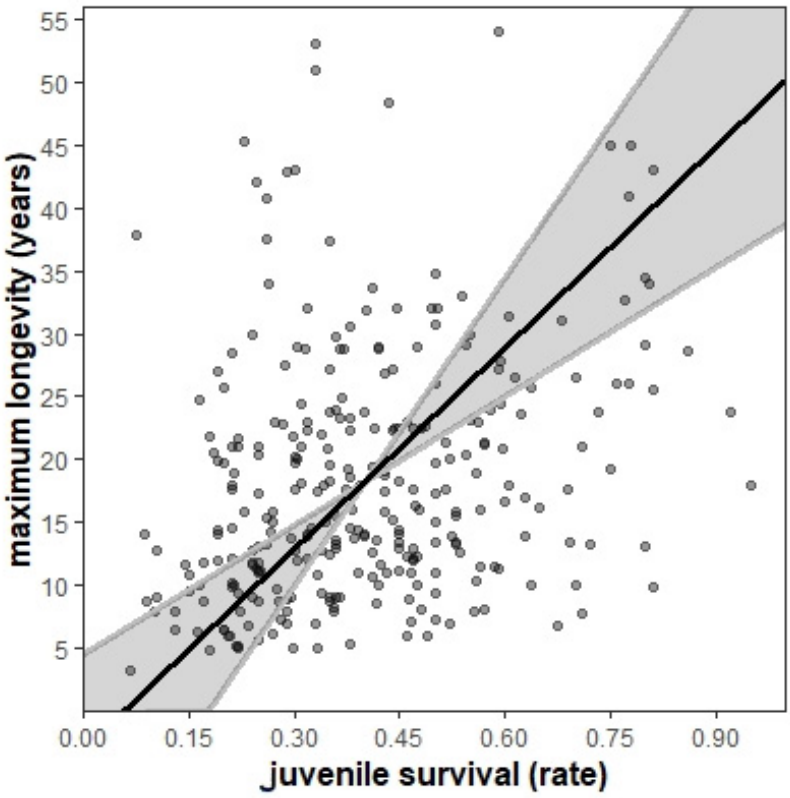

Figure 1 | Correlation between juvenile survival (first-year survival) and maximum longevity on 293 bird species.

RMA slope = 53.15, 95% CI (34.13, 81.71); $r_{Spearman}$ = 0.28, S = 3003600, p <0.0001. 64 species (22%) are inside and 229 (78%) outside the 95%CI of the regression line (shaded area). See Fig. S6 for species identification.

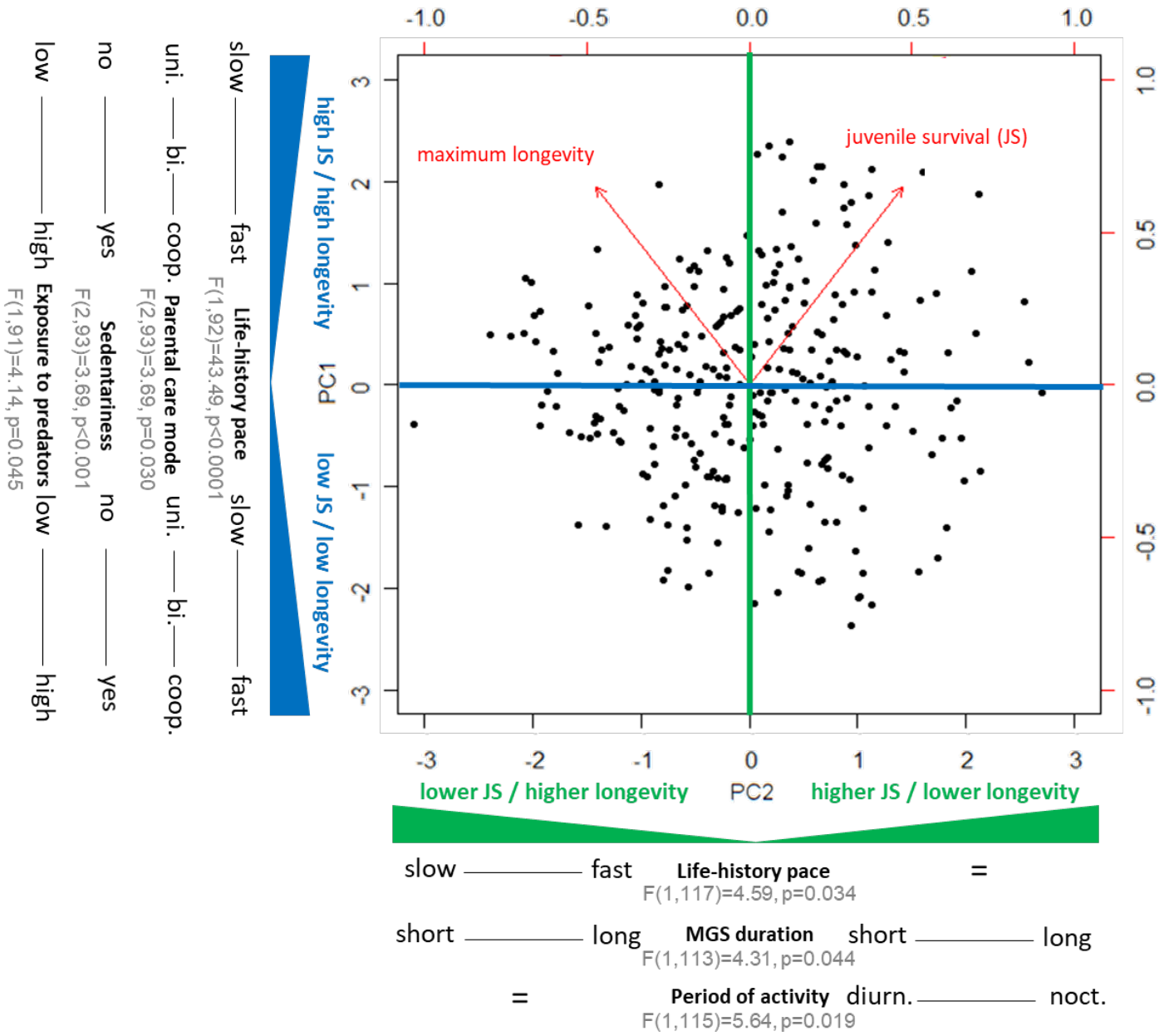

Figure 2 | Correlates of the positive (PC1) and mismatching (PC2) combinations of juvenile survival and longevity. Graphical summary of the main results from the backward model selections on phylogenetically controlled linear mixed models investigating which life-history, ecological and social traits characterised species with different combinations of juvenile survival (first-year survival) and longevity (N=204).

The blue axis (PC1) represents combinations that concur with tETA's classical prediction (high juvenile survival associated with high longevity or vice versa). The green axis (PC2) represents combinations that deviate from tETA's classical prediction (deviation towards higher juvenile survival associated with lower longevity or vice versa). Graphics of each independent results are provided in Figs. S8 and S9. See Fig. S10 for species identification and Fig. S11 for order identification.

JS = juvenile survival, Coop. = cooperative breeding, bi. = biparental care, uni. = uniparental care, noct. = nocturnal, diurn. = diurnal, F(…,...) = Conditional F statistic and its degrees of freedoms averaged over the 300 models, p = averaged p value over the 300 models.