Inter-specific variation of maternal thyroid hormones associate with migration, mode of development, and captivity: a phylogenetic comparative analysis

Bin-Yan Hsu[1], Veli-Matti Pakanen[2,3], Winnie Boner[4], Tapio Eeva[1], Blandine Doligez[5], Ton G.G. Groothuis[6], Erkki Korpimäki[1], Toni Laaksonen[1], Asmoro Lelono[6], Pat Monaghan[4], Tom Sarraude[1,6], Barbara Tschirren[7], Robert L. Thomson[8], Jere Tolvanen[2], Rodrigo A. Vásquez[9], Suvi Ruuskanen[1]

[1] Department of Biology, University of Turku, Finland

[2] Ecology and Genetics Research Unit, University of Oulu, Finland

[3] Department of Biological and Environmental Sciences, University of Gothenburg, Sweden

[4] Institute of Biodiversity, Animal Healthy and Comparative Medicine, University of Glasgow, Scotland, United Kingdom

[5] Department of Biometry and Evolutionary Biology, CNRS UMR 5558, Université de Lyon 1, France

[6] Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, the Netherlands

[7] Centre for Ecology and Conservation, University of Exeter, United Kingdom

[8] Fitzpatrick Institute of African Ornithology, University of Cape Town, South Africa

[9] Instituto de Ecologíay Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile

Abstract

Animals' life-history traits vary largely along many continuums across species and several physiological parameters have been proposed as possible mediators that drive the life-history variation, such as metabolic rates, glucocorticoids, and oxidative stress. Interestingly, thyroid hormones (THs), despite closely interacting with these physiological parameters, have never been considered as such mediators. Because of the crucial effects on embryonic development, THs can also induce transgenerational plasticity when transferred into developing offspring, for instance, via egg yolks in birds. In this study, we compiled a unique data set of maternal yolk THs in 34 bird species across 17 families and 6 orders and analysed them with data of life-history traits along several life-history continuums. Our phylogenetic mixed models estimated higher deposition of the two most important forms of THs – T3 and T4 -- in both concentrations and total amounts in migratory species than resident species, and larger total amounts of T3 in precocial species than in altricial species. However, maternal THs did not show clear associations with any traits of the pace-of-life syndrome. When taking environmental factors into account, we found that captive species also deposited higher TH concentrations and larger amounts in the egg yolks than wild species. These findings suggest that THs are likely involved in the evolution of life-history variation or vice versa. Accordingly we proposed many angles for further studies.

Key words: life histories, birds, maternal thyroid hormones, phylogenetic comparative analysis

38 **Introduction**

39 Life-history variation constitutes a large part of biodiversity. Across species, life-history traits are
40 often inter-correlated and present along several continuums. For example, many life-history traits,
41 such as lifespan, co-vary with one another and constitute a continuum representing the 'pace of life'
42 (Ricklefs and Wikelski 2002; Dammhahn et al. 2018). On the one end of this continuum, species
43 exhibit faster growth and development, earlier maturation, but faster senescence and shorter
44 lifespan ("fast" species). On the other end, species have slower growth and development, later
45 maturation and first reproduction, but also live longer ("slow" species). Other life-history
46 continuums, such as the nutrient source for developing embryos (from yolk or via placenta), income
47 versus capital breeders, precocial to altricial developmental modes, and various degrees of
48 migratory tendencies, also exist across various taxa in the animal kingdom.

49 Identifying the mechanisms underlying the evolution of life history differences has
50 fascinated evolutionary biologists for decades. For example, for the pace-of-life (POL) continuum,
51 metabolic rate has been proposed as a mediator as it exhibits a parallel pattern with fast species
52 usually having higher basal and resting metabolic rates (BMR and RMR), while slow species having
53 lower metabolic rates (e.g. Wikelski et al. 2003; Auer et al. 2018). Some studies also proposed other
54 possible mediators, such as glucocorticoids (Hau et al. 2010), oxidative stress (Vágási et al. 2019),
55 and blood glucose level (Tomasek et al. 2019). We propose a novel prediction that thyroid hormones
56 (THs) could be one of the underlying mechanisms explaining the life-history variation, such as the
57 POL continuum. This prediction is likely because THs have regulatory functions on metabolism
58 (Mullur et al. 2014) and interactions with glucocorticoids (Darras et al. 1996; Kulkami and Buchholz
59 2012; Cortés et al. 2014), yet it is surprising that no studies have yet explored the possibility.

60 Not only regulating metabolisms in adult animals, THs are also transferred from mothers to
61 developing offspring in all vertebrates (Ruuskanen and Hsu 2018). Such maternally-derived THs
62 (hereafter "maternal THs") play an indispensable role for early embryonic development (Moog et al.
63 2017; Darras 2019). In humans, the levels of maternal THs are associated with new-born body mass

64 and children's IQ (Medici et al. 2013; Korevaar et al. 2016). This suggests the variation in maternal
65 THs can induce transgenerational phenotypic plasticity, which can constitute an important part of
66 phenotypic variation also in wild animals (Mousseau and Fox 1998; Moore et al. 2019). Nevertheless,
67 the ecological and evolutionary significance of maternal THs in wild animals was almost totally
68 neglected (Ruuskanen and Hsu 2018). Recently, several experimental studies manipulating maternal
69 THs reported inconsistent effects of yolk TH on nestling traits across species (Ruuskanen et al. 2016a;
70 Hsu et al. 2017, 2019a). Such species differences intrigue us to consider the possibility that maternal
71 yolk THs might have co-evolved with life-history differences and therefore species respond to
72 elevated yolk THs differently.

73 In this study, we explored the potential role of maternal yolk THs underlying the continuums
74 of life-history strategies in birds by collecting eggs from 34 species of birds and analysing THs in the
75 egg yolks. In birds, two maternally derived THs – triiodothyronine (T3) and thyroxine (T4) are
76 transferred and stored in the egg yolk (Sechman and Bobek 1988; Prati et al. 1992). We asked
77 whether the inter-specific variation of yolk THs would associate with life-history traits across species,
78 in the meanwhile taking into account some environmental factors that may potentially contribute to
79 the variation in yolk THs. The associations between maternal THs and life-history traits, if exist,
80 probably reflect the involvement of maternal THs in the evolution of life-history differences or vice
81 versa.

82 Based on the known functions of THs, we considered three life-history continuums, along
83 which we hypothesized that maternal yolk THs may be associated with the related life-history traits.
84 The first is the altricial-precocial developmental spectrum. At the two ends of this life-history
85 continuum, precocial species and altricial species show distinctive ontogenetic patterns of visual and
86 locomotory ability (Starck and Ricklefs 1998c), hypothalamic-pituitary-adrenal (HPA) axis (Wada
87 2008), hypothalamic-pituitary-thyroid (HPT) axis (McNabb 2006; de Groef et al. 2013) and
88 thermoregulation (Price and Dzialowski 2018). Specifically, in precocial species, the thyroid function
89 already starts in the middle of incubation and the TH levels in thyroid gland and blood circulation

both peak around hatching. By contrast, in altricial species, the thyroid function only starts days after hatching, and the blood circulating TH levels slowly increase towards the adult level (McNabb 2006; de Groef et al. 2013). Therefore, we hypothesized that such differences in the mode of development may be associated with yolk TH levels, either because higher maternal THs are required for a comparatively advanced development at hatching or because the developmental modes at least partly determines the transferring process of maternal THs, or both .

Second, we considered the life-history differences between migratory and resident species. THs have been known to regulate seasonal physiology and reproduction (Dardente et al. 2014; McNabb and Darras 2015; Nishiwaki-Ohkawa and Yoshimura 2016) and also moulting and feather regeneration (Vézina et al. 2009; Pérez et al. 2018). Several studies have also considered THs as part of the hormonal mechanism underlying migration (Pérez et al. 2016). We thus hypothesized that maternal TH levels may be associated with species' migratory status.

Third, we considered the slow-fast pace-of-life (POL) continuum (Ricklefs and Wikelski 2002; Dammhahn et al. 2018). As introduced above, metabolic rates (Wikelski et al. 2003; Auer et al. 2018), glucocorticoids (Hau et al. 2010), and oxidative stress (Vágási et al. 2018) have been proposed to mediate the POL-related life-history variation. Interestingly, THs appear to have associations with all of them. It is well known that THs have regulatory function on metabolism (Mullur et al. 2014), and in wild birds, within-species studies have confirmed positive correlations between blood THs and BMR and RMR (e.g. Chastel et al. 2003; Elliott et al 2013; Welcker et al. 2013). THs also have cross-talks with the HPA axis (Cortés et al. 2014) and may induce higher oxidative stress due to the metabolic effects (Villanueva et al. 2013). Therefore, it seems possible that THs may also be a mediator of pace of life.

In addition to life-history differences, some environmental factors may also contribute to the inter-specific variation of maternal yolk THs and should be taken into account. First, we expected that the foraging environment, through its direct influence on food composition, may influence the inter-specific variation of maternal yolk THs. In a previous study with captive wild-type rock pigeons

116 (*Columba livia livia*), food conditions before and during egg-laying were indeed found affecting
117 maternal yolk TH levels (Hsu et al. 2016). One possible explanation to this finding probably lies on
118 the iodine content in the diet, as iodine is an essential ingredient for TH production (Bizhanova and
119 Kopp 2009). In humans, even mild iodine deficiency during pregnancy has been shown to lead to
120 deficiency of maternal T4 and hence negative effects on foetal development (Bath et al. 2013;
121 Trumpff et al. 2013). In wild animals, previous studies have also found that environmental iodine
122 availability is associated with antler weights of roe deer (*Capreolus capreolus*) via its influence on TH
123 production (Lehoczki et al. 2011), and freshwater alligators (*Alligator mississippiensis*) have on
124 average lower plasma T3 and T4 concentrations than the estuarine conspecifics (Boggs et al. 2011).
125 Therefore, we hypothesized that iodine availability from the environment and diet (e.g. Eckhoff and
126 Maage 1997) could contribute to part of the variation in maternal yolk THs. Moreover, captive
127 environment differs in many aspects from a wild environment, such as food availability and safety
128 from predators. The confinement and regular human disturbance might also pose as chronic
129 stressors, which may influence THs (e.g. Angelier et al. 2016) and therefore maternal TH deposition.
130 We therefore hypothesized that captivity may also have influence on maternal yolk THs.
131 To test these hypotheses, we collected related life-history traits pertaining to each
132 hypothesis from the literature. The environmental variables were assigned based on the sampled
133 population. Using birds as a model system, we measured maternal THs in egg yolks from 34 species
134 across 17 families and 6 order, using a nano-LC-MS/MS protocol (Ruuskanen et al. 2018),
135 constructing the first and unique interspecific maternal TH data set. Combining the data of life-
136 history traits and maternal THs, we were able to run phylogenetic mixed-effects models using a
137 Bayesian framework to test our hypotheses. Potentially,

Materials and Methods

Sample collection

We collected unincubated eggs from 34 species of birds across 17 families and 6 orders (n = 1-21 per species, median=7, Table S1). Nests of wild species were located by extensive nest searches in the known breeding habitats of each species or from nest-box populations during 2016-2017. We aimed at collecting eggs from species with varying body sizes and life-history traits and included both precocial and altricial species. All eggs were collected before clutch completion (i.e. when found, the eggs were cold and clutch was not completed) and one, randomly sampled egg per clutch was collected. Therefore, in most of the cases, the laying order of the sampled egg was unknown. Most of the wild species were sampled from Finnish populations near Turku (60°27'N, 22°16'E), Oulu (65°01'N, 25°28'E) and Kauhava (63°06'N, 23°04'E) regions, except thorn-tailed rayaditos (*Aphrastura spinicauda*, sampled mostly from Chiloé island, Chile, 42°40'S, 73°59'W) and collared flycatchers (*Ficedula albicollis*, from Burgsvik, Gotland, Sweden, 57°02'N, 18°16'E). The eggs of captive homing pigeons (*C. l. domesticus*) and domesticated chicken (*Gallus gallus domesticus*) and eggs of semi-captive pheasants (*Phasianus colcichus*) and grey partridges (*Perdix perdix*) were sampled from local breeders in Finland. The eggs of red jungle fowl (*G. g. gallus*) and rock pigeons (*C. l. livia*) were sampled from the captive colonies at the University of Groningen, the Netherlands, and the eggs of captive zebra finches (*Taeniopygia guttata*) were from the University of Glasgow, UK. All collected eggs were first frozen and stored at -20°C until further analysis. For most of the species, the frozen eggs were shipped to the University of Turku, where we separated the yolk for hormone analysis (see *Yolk TH analysis*). Two exceptions are the collared flycatchers and the rock pigeons, for which the eggs had been dissected and the yolk had been homogenized and mixed in known amount of milli-Q (MQ) water before shipped to University of Turku and were already ready for extraction. Eggs of wild species were collected under licenses from the environmental authorities in each country: Finland, VARELY/665/2016, POPELY/61/2016, VARELY/63/2016, VARELY/412/2016, VARELY/6085/2016, and Finnish Wildlife Agency 84/2016; Chile, Agricultural Ministry 404/2017,

164 Sweden, National Board for Laboratory Animals. Captive species were housed and eggs were
165 collected following all national and international guidelines
166
167 Yolk TH analysis
168 We extracted THs from the egg yolks and measured two THs (T3 and T4) at the University of
169 Turku and Turku Centre of Biotechnology. Yolk was separated from albumen after a short period of
170 thawing. Few eggs showed signs of very early development and all such eggs were discarded from
171 the analysis. After dissection, yolks were weighed (~0.01 g), and a half (for passerines) or a quarter
172 (for other species) of the yolk was weighed for extraction and we added an equal amount of MQ to
173 facilitate homogenizing.
174 We used the extraction protocol described previously (Ruuskanen et al. 2016b). In brief, we
175 first added 2 ml methanol to the yolk-MQ mixture (ca. 300 mg) and homogenized the sample. A
176 known amount of $^{13}C_{12}$-T4 (Larodan) was added to each sample as an internal tracer, which allowed
177 us to correct for extraction efficiency (i.e. recovery). Four ml of chloroform was then added and
178 samples were centrifuged at +4°C 1900g for 15 min. The supernatant was then collected and the
179 pellet was re-extracted in 2:1 chloroform-methanol mixture, back-extracted with 0.05% $CaCl_2$ into
180 aqueous phase, and re-extracted with chloroform:methanol:0.05% $CaCl_2$ mixture (3:49:48). The
181 aqueous phase was further purified on Bio-Rad AG 1-X2 resin columns, eluted with 70% acetic acid,
182 and then vacuum-evaporated overnight. Samples from different species were spread over extraction
183 batches and the extraction batch ID was included as a random intercept in the statistical models.
184 We used a validated nano-flow liquid chromatography-mass spectrometry (LC-MS) protocol
185 to measure yolk T3 and T4 simultaneously (Ruuskanen et al. 2018). In brief, the dry TH extracts were
186 re-suspended in 150 µl 0.1% NH_3 and further diluted with 0.01% NH_3. The dilution factor depended
187 on the expected amount of T3 and T4 in each sample. Internal standards $^{13}C_6$-T3 and $^{13}C_6$-T4 were
188 added to identify and also quantify T3 and T4 in the samples. A triple quadruple mass spectrometer
189 (TSQ Vantage, Thermo Scientific, San Jose, CA) and nano-flow HPLC system Easy-nLC (Thermo

190 Scientific) were used for the measurements. The on-column quantification limits were 10.6 amol and
191 17.9 amol for T4 and T3, respectively (Ruuskanen et al. 2018). The data was acquired automatically
192 using Thermo Xcalibur software (Thermo Fisher Scientific) and subsequently analysed by Skyline
193 (MacLean et al. 2010). TH concentrations were calculated using the peak area ratios of sample to
194 internal standard, corrected for recovery, and expressed as pg/mg yolk. We further calculated the
195 total amount of THs per yolk and expressed it as ng/yolk.
196
197 Life-history traits and environmental factors
198 *I. Altricial-Precocial continuum*
199 We specified all our species' **developmental mode** as either precocial or altricial, following Starck
200 and Ricklefs (1998a). We only had four semi-precocial species in our data set, which all belong to the
201 family Laridae (gulls and terns) and only one semi-altricial species (the kestrel, *Falco tinnunculus*).
202 Therefore, semi-precocial and semi-altricial species were pooled with precocial or altricial species,
203 respectively.
204
205 *II. Migratory versus resident species*
206 Species' **migratory status** was categorized as either migratory or resident, determined mainly
207 according to the data compiled in Lehikoinen et al. (2003), McNab (2009) and Pap et al. (2015).
208 When in contradiction, the assignment was made based on the population from which we collected
209 eggs.
210
211 *III. Pace-of-life continuum*
212 The pace-of-life history continuum incorporates many related life-history traits, including a species'
213 developmental duration, fecundity, metabolic rate, growth rate, and the rate of maturation and
214 senescence.

215 (i) The data on **developmental duration** was collected mainly from the amniote life-history
216 database compiled by Myhrvold et al. (2015) with supplementation from other literature
217 (see *supplementary materials*). We collected the **incubation duration** and **the time to**
218 **fledging** (from hatching) to represent the prenatal and postnatal part of the developmental
219 period. We additionally calculated two more variables: **the total length of development**
220 (incubation duration + time to fledging) and **the proportion of prenatal development**
221 (incubation duration / total developmental length).
222 (ii) The **growth rate** data originated from the data set in Starck and Ricklefs (1998b) and
223 supplemented with other literature (see *supplementary materials*). For comparability, the
224 logistic growth rate constants were used to represent the growth rate of each species.
225 Whenever multiple sources of the growth rates are available for a species, an average was
226 calculated and used.
227 (iii) **Species' body mass, clutch size** and **number of clutches per year** were obtained from
228 Myhrvold et al. (2015).
229 (iv) The data of **basal metabolic rates** (BMR) was mainly obtained from McKechnie et al. (2006)
230 and McNab (2009), supplemented by other literature (see *supplementary materials*).
231 (v) **Maximum lifespan** and **ages at first reproduction** originated from the database AnAge
232 (Tacutu et al. 2013), except for the thorn-tailed rayaditos (*Aphrastura spinicauda*), for which
233 the data was derived from the unpublished data by R.A. Vásquez et al.
234
235 *IV. Environmental factors*
236 For environmental factors, we created two variables to represent species' **foraging environment** and
237 **captivity.** Respectively, species were categorized as marine-bound (foraging on marine food
238 resources) or terrestrial (foraging on non-marine bound resources) based on the breeding territory
239 and diet, and wild or captive. Semi-captive species (the pheasant and the grey partridge) were
240 categorized as captive.

All life-history and environmental data we compiled for this study, as well as the sources we consulted, the final values used in all our models, will be provided in the supplementary materials or deposited in a public repository.

Phylogenetic mixed models

Model specifications

Following Hadfield and Nakagawa (2010), we ran phylogenetic mixed models with the R package *MCMCglmm* (Hadfield 2010). T3 and T4 concentrations (pg/mg yolk) as well as total contents (ng/yolk) were ln-transformed and standardized and used as dependent variables in separated univariate models. Species body mass and other life-history and environmental variables (see *Life-history traits and environmental factors*) were treated as fixed factors and covariates. In order to facilitate model fitting, body mass was also ln-transformed and standardized. Before fitting models, all two-level categorical variables were first dummy-coded as -0.5 and 0.5 (Table S2), to facilitate model mixing/convergence. The life-history traits that are known to be associated with body mass (BMR, growth rate, maximum lifespan, and age at first reproduction) were first corrected for body mass and phylogenetic relatedness among species using the R package *phytools* (Revell 2009, 2012). BMR data, in particular, was first converted to mass-specific BMR and ln-transformed and corrected for size and phylogeny.

The four variables of developmental duration were strongly correlated with one another. Therefore, we did a phylogeny-corrected principal component analysis (PCA) using R package *phytools* (Revell 2009, 2012). The first two PCs explained 99.74% of the variance (Table S3). The loadings suggested that PC1 is highly positively correlated with the time to fledging and the total length of developmental period, and negatively correlated with the proportion of prenatal development, while PC2 is negatively correlated with the duration of prenatal development (Table S3). In subsequent phylogenetic mixed models, we therefore used the scores of PC1 and PC2 for each species to represent the developmental duration.

267 Because the data of life-history traits was not available for all species, we defined several
268 sets of models depending on data availability, listed in Table 1. Each model and data set was thus
269 pruned for the specific set of species where data was available. Each model set consists of separate
270 models to analyse the concentrations as well as total contents of T3 and T4, respectively. This is
271 because in oviparous species, the total contents of maternal hormones in the yolk is fixed after yolk
272 formation. Therefore, the total content of hormones represents an initial maximum hormone
273 availability and may represent some different biological meanings from the concentration.
274 In all models, the phylogenetic relatedness among all species included was treated as
275 random effects, following Hadfield and Nakagawa (2010). Additionally, species name was also
276 included as a random factor to control for within-species non-independence among the multiple
277 eggs from the same species. For this random factor, homing pigeons and domesticated chickens
278 were coded separately from their wild-type ancestor rock pigeons and red jungle fowl, despite that
279 they were not distinguished in the phylogeny (i.e. treated as they same species, *Columba livia* and
280 *Gallus gallus*). The batch of hormone extraction was also included as an additional random factor.
281 Response variables were all assumed to follow Gaussian distributions. All models were run for
282 750000 iterations with a 350 thinning interval and burn-in of 50000, aiming for an approximately
283 2000 effective sample size for all parameters. Following Houslay and Wilson (2017), we used an
284 uninformative parameter-expanded prior following a Cauchy distribution (V=1, nu=1, alpha.mu=0,
285 alpha.V=25^2) for all random factors. Tests using an uninformative invert-Wishart prior or improper
286 flat prior gave qualitatively same results, suggesting the results are robust against the choice of
287 priors.
288
289 *Phylogenetic trees and phylogeny uncertainty*
290 Each phylogeny set (Table 1) was correspondingly pruned and obtained from BirdTree.org (Jetz et al.
291 2012) based on two phylogenetic backbones (Ericson et al. 2006; Hackett et al. 2008). For each
292 backbone, 100 possible trees were generated and downloaded. All models were tested repeatedly

293 across the 100 possible trees in each backbone and the posterior means of parameter estimates and
294 their 95% credible intervals (CIs) were stored. The average posterior mean and the average
295 boundaries of the 95% CIs were calculated to account for phylogenetic uncertainty (Rubolini et al.
296 2015) and reported. The results are highly similar across all possible trees (see Fig. S1 for examples)
297 and between the two backbones. Therefore we only reported the results based on the Hackett
298 backbone.
299
300 *Model diagnostics*
301 As models across all possible phylogenetic trees produced highly similar results, we examined model
302 performance by re-fitting all models with a consensus tree. The consensus tree was derived using
303 the R package *phytools* (Revell 2012) for each phylogeny set. Model diagnostics were conducted by
304 visual inspection on the trace plots for proper mixing and on autocorrelations. Model convergence
305 was also checked using Gelman diagnostics provided in the R package *coda* (Plummer et al. 2006).
306 For all models, visual inspection did not raise any red flags for poor mixing or substantial
307 autocorrelation and all models passed the Gelman diagnostics with all potential scale reduction
308 factors < 1.05.
309
310 *Phylogenetic signals*
311 Phylogenetic signal, a.k.a. phylogenetic heritability (H^2), was calculated as
312 $$H^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_s^2 + \sigma_b^2 + \sigma_e^2}$$
313 where σ_a^2 represents the variance of the phylogeny; σ_s^2 represents the variance accounted by
314 individual species; σ_b^2 represents the variance of hormone extraction batches; σ_e^2 represents the
315 residual variance. The H^2 calculated this way is equivalent to the Pagel's λ (Hadfield and Nakagawa
316 2010).

317 Because phylogenetic signal is in fact the proportion of the phylogenetic variance over the
318 total variance of all random effects, the fixed factors included in the model will influence the value of
319 the phylogenetic signal by changing the residual variance. Therefore we calculated the phylogenetic
320 signals for yolk T4 and T3 based on the phylogenetic mixed model that only included the life-history
321 traits whose 95% CIs did not encompass 0 (i.e. having credible associations). These are the
322 developmental mode, migratory status, captivity, and body mass (see *Results*). In these models, all
323 34 species and the full phylogeny set was included and we used a consensus tree from the Hackett
324 backbone, derived by using the *phytools* package (Revell 2012).
325
326 **Table 1.** Model, phylogeny and data sets defined in this study

Model set	Phylogeny	Data set	Model structure (fixed factors)	Remark
1	All 34 species	Full data set	~developmental mode + migration + body mass + maximum lifespan + foraging environment + captivity	
2a	Excluding *Coturnix japonica**	Excluding domesticated Japanese quails and domesticated chicken	~developmental mode + migration + body mass + clutch size + clutches per year + captivity	Domesticated quails and chicken do not lay clear "clutches" of eggs.
2b	Excluding *Coturnix japonica*	Excluding Japanese quails	~developmental mode + migration + body mass + PC1 and PC2 of developmental period + captivity	Time to fledging data was missing for Japanese quails
3	Excluding *Gallus gallus*	Excluding red jungle fowl and domesticated chicken	~developmental mode + migration + body mass + age at first reproduction + captivity	Age at first reproduction data was missing for both jungle fowl and chicken
4	28 species with BMR data	Species with BMR data	~developmental mode + migration + body mass + BMR + captivity	
5	29 species with growth rate data	Species with growth rate data	~developmental mode + migration + body mass + growth rate + captivity	

* In Model set 2a, both Japanese quails and domesticated chicken were removed from the “data set” but only *Coturnix japonica* was removed from the phylogeny because *Gallus gallus* was still needed in the phylogeny for the data from red jungle fowl.

330 **Results**

331 Inter-specific variation in yolk THs and phylogenetic signals

332 Among the 34 species, we observed a substantial inter-specific variation in both T3 and T4
333 concentrations (Fig. 1, Table S1). Great tits (*Parus major*) and redshanks (*Tringa totanus*) had the
334 lowest and highest concentrations of yolk T3 and T4 among the 34 species, respectively. Between
335 the two species, the difference in average yolk THs reached 100-fold for T3 (great tit, mean±SD =
336 0.112±0.032 pg/mg yolk, n=11; redshank, mean±SD = 11.242±5.067 pg/mg yolk, n=4), and also
337 reached 18-fold for T4 (great tit, mean±SD = 0.989±0.292 pg/mg yolk, n=12; redshank, mean±SD =
338 18.101±4.125 pg/mg yolk, n=4).

339 The moderate to strong phylogenetic signals indicated that the phylogenetic relatedness
340 among species accounted for 50%-75% of the inter-specific variation in yolk THs (Table 2). On
341 average, T3 has stronger phylogenetic signals although their 95% CIs overlapped.

342

343 **Table 2.** Phylogenetic signals (i.e. phylogenetic heritability) for maternal yolk T3 and T4.

Hormone	Parameter	Posterior mean [95% CI]
T3	concentration	0.76 [0.56, 0.93]
	total content	0.77 [0.57, 0.90]
T4	concentration	0.49 [0.16, 0.79]
	total content	0.65 [0.42, 0.87]

344

345 Associations between yolk THs and life-history variables

346 The estimated posterior means and 95% CIs from all models are collected in Fig. 2. Precocial
347 species clearly deposited larger total amounts of THs in the egg yolks than altricial species (Fig. 3).
348 The model set 1 supported this difference with positive posterior means and 95% CIs, when
349 controlling for species body mass and other covariates, especially for T3 contents (Fig. 2D). Also,
350 migratory species generally deposited higher concentrations and also larger amounts of both THs in
351 the egg yolks than resident species (Fig. 4), which were supported by the model set 1 (Fig. 2). Species
352 body mass also strongly correlated with yolk TH content, but not with yolk TH concentration (Fig. 2).

353 Along the slow-fast pace-of-life continuum, however, no traits were found to be credibly associated
354 with maternal yolk THs (Fig. 2)
355
356 Associations between yolk THs and environmental variables
357 Between terrestrial and marine-bound species, although the raw data showed that marine-bound
358 species apparently deposited more yolk THs (Fig. 5), this was not supported by the phylogenetic
359 mixed models (Fig. 2). Between captive and wild species, credible differences in both yolk T3 and T4,
360 and in both concentrations and total contents (Fig. 2) were found. This suggested that captive
361 species deposit higher concentrations and larger amounts of yolk THs than wild species (Fig. 6).

362 **Discussion**

363 Maternal THs and life-history variation

364 Among the three life-history continuums, our phylogenetic mixed models estimated
365 credible differences of maternal yolk THs between the migratory and resident life histories, and
366 between precocial and altricial developmental modes. However, contradicting to our expectation,
367 none of the pace-of-life (POL) related traits were found credibly associated with maternal yolk THs,
368 after controlling for body mass. The moderate to strong phylogenetic signals also indicate that a
369 substantial proportion of variation in maternal THs is accounted by the phylogeny itself. This
370 suggests a substantial extent of phylogenetic inertia, which may present some evolutionary
371 constraints in maternal TH deposition. Despite the constraint, the credible differences of maternal
372 TH between precocial and altricial species, and between migratory and resident species still suggest
373 that maternal THs are involved in the evolution of these two life-history continuums or vice versa.

374

375 *THs and migration*

376 Migration is a critical and demanding life-history stage. Many physiological changes are
377 occurring both before and after migration, such as fat deposition, gonadal regression and
378 recrudescence. The temporal overlap with other seasonal activities, such as breeding and moult, also
379 tends to be minimized over evolutionary history in migratory species (Hahn et al. 2015). By contrast,
380 resident species usually have a relatively longer time window to coordinate the physiological
381 transition before and after reproduction compared with migratory species. Therefore, migratory
382 species may require a higher sensitivity or accuracy to fine-tune the transition. Our result of higher
383 yolk TH levels, not only in terms of higher concentrations but also larger amounts, in migratory than
384 resident species probably suggest prenatal programming effects on the coordination of such annual
385 schedule. THs play a central role in the molecular mechanisms of photoperiodic response. The
386 photoperiodic change influences the expression levels of the thyroid-stimulating hormones (TSH) in
387 the hypothalamus, which subsequently induces reciprocal switching of two deiodinases (DIO2,

388 converting T4 to active T3 and DIO3, converting T4 and T3 to inactive THs) that activate and
389 inactivate T3, respectively (Nakao et al. 2008; Dardente et al. 2014). This photoperiodic DIO2/DIO3
390 expression pattern further regulates the seasonal maturation of gonads. Interestingly, in a study of
391 great tits, the photoperiodic DIO2/DIO3 gene expression pattern was only evident in a Swedish
392 population but not in a southern German population (Perfito et al. 2012). This difference therefore
393 seems to suggest a higher sensitivity to photoperiodic change in a northern population, where the
394 appropriate time window to breed is shorter. Difference in maternal THs could have some
395 organizational effects on TH responsiveness later in life. There may be still species differences in the
396 seasonal regulation of DIO2/DIO3 expression, as a similar pattern was not found in European
397 starlings (*Sturnus vulgaris*, Bentley et al. 2013). Comparison of TH-related gene expression between
398 conspecific populations that possess different migratory propensity, potentially in combination with
399 TH manipulation, will probably help identify the elements responsible for such differences.
400
401 *Precocial development requires more maternal THs?*
402 The result that precocial species deposited higher amounts of THs, particularly T3, in the egg
403 yolks than altricial species fits well in line with their distinct developmental trajectories (Starck and
404 Ricklefs 1998c). Compared with precocial species, altricial species seem to temporally shift their
405 physiological maturity to a later life stage in visual and locomotory ability (Starck and Ricklefs 1998c),
406 HPA and HPT axis (McNabb 2006; Wada 2008; de Groef et al. 2013) and thermoregulation (Price and
407 Dzialowski 2018). Our result appears to suggest the requirement of a larger amount of maternal THs
408 for such an advanced ontogenetic trajectory in precocial birds.
409 An alternative way to look at the contrasting ontogenetic differences between precocial and
410 altricial development may be the placement of hatching on the ontogenetic timeline. Regardless of
411 the developmental modes, the event of hatching requires a lot of physiological changes to prepare
412 the young for the “outside” world and therefore marks a major life-stage transition. As the altricial
413 developmental mode is assumed to evolve later than the precocial mode (Starck and Ricklefs 1998c;

414 de Groef et al. 2013), one way to look at the shift is that the event of hatching is moved "leftwards"
415 along the ontogenetic timeline in the altricial development so that hatching occurs earlier when the
416 young is still poorly developed. Whether maternal THs mediates such a shift during the evolution
417 from precocial to altricial development requires further studies, but according to our data such a
418 change may coincide with a reduction in TH deposition over the course. We therefore could expect
419 intermediate levels of maternal THs in semi-precocial and semi-altricial species. Interestingly, the
420 only semi-altricial species we have measured, the Eurasian kestrel, indeed has higher maternal TH
421 content than most other altricial species, but lower than most semi-precocial and precocial species
422 (Fig. 3).
423 Unlike the differences between migratory and resident species, only the total content of THs
424 was found associated with the developmental mode. We reiterate here that our model has
425 accounted for species body mass, so the result is not due to the generally larger body size in
426 precocial species. This therefore suggests that for some traits it may be the total content that
427 matters, instead of the *per capita* amount (i.e. concentration).
428
429 *No size-independent associations between maternal THs and pace of life (POL)*
430 Given the known function of THs on metabolism and interactions with glucocorticoids, it is
431 surprising that we did not detect any obvious associations between maternal THs and all tested POL-
432 related traits (Fig. 2). Although yolk TH contents show strong correlations with species body mass,
433 this is because large species produce large eggs and large yolks, hence higher total amounts of yolk
434 THs. After controlling for body mass and phylogenetic relatedness, only clutch size showed a
435 potential trend with T4 contents. The model estimated a negative posterior mean and the 95% CI
436 was slightly overlapped with 0 (Fig. 2B), implying that species with larger clutch sizes tended to
437 deposit less T4 in the egg yolks. Such a trend is probably driven by the difference between
438 passerines and shorebirds (Fig. S2). Confirming such a relationship perhaps would require a larger
439 sampling scheme that includes more species.

440 Our hypothesis that maternal THs may be associated with POL is based on the relationships
441 of blood THs with glucocorticoids and with metabolic rates. The lack of associations between
442 maternal THs and POL-related traits therefore probably implies that the effects of maternal THs
443 cannot be translated directly to blood THs. This could be due to limited organizational effects of
444 maternal THs on the HPT axis or more complex manifestation, such as sex-specific effects. To our
445 knowledge, there is currently only a couple of experimental studies that have examined how
446 maternal THs influenced blood THs and metabolic rates during the nestling phase. In the great tits,
447 yolk TH elevation did not influence nestling RMR before fledging (Ruuskanen et al. 2016a). In the
448 rock pigeons, similar yolk TH elevation raised the RMR in female nestlings but reduced it in males on
449 the hatching day, a pattern that was consistent with the effects on plasma T4 concentrations (but
450 not T3) at day 14 after hatching (in the middle of the nestling phase, Hsu et al. 2017). Although in the
451 pigeon study, elevated yolk THs showed consistent effects on nestling RMR and plasma T4, the sex-
452 specific pattern remains unexplained. Nevertheless, a previous study in domesticated chicken
453 embryos does show that the injection of THs into the yolk influenced the expression of the TH-
454 transporters in the brain (van Herck et al. 2012). This suggests that differential exposure to maternal
455 THs may influence brain TH availability. Such changes might have a potential to alter the sensitivity
456 and responsiveness of the HPT axis for a long term. Therefore, so far the notion that that maternal
457 THs may organizationally shape the HPT axis have not received substantial support but for the
458 moment cannot yet be ruled out. Another possibility to explain the lack of associations between
459 maternal THs and POL-related traits is that blood THs do not have such associations. This would be
460 quite surprising considering the close associations between THs with metabolic rates,
461 glucocorticoids, and oxidative stress, but after all such a possibility has not yet been confirmed or
462 falsified by far.
463
464 *Maternal THs and life-history variation: cause or consequence?*

465 We have discussed our results as maternal THs could be a mediator over the evolutionary course of
466 the life-history differences. However, it could be the physiological differences between migratory
467 and resident life histories, and between precocial and altricial developments that result in
468 differential maternal TH deposition during egg formation across species. So far, the physiological and
469 molecular mechanism of yolk hormone deposition in birds is still unclear. However, some
470 circumstantial evidence have suggested that yolk TH deposition does not reflect blood TH variation
471 (Hsu et al. 2016) and some regulatory mechanism of yolk TH deposition possibly exists. Thus
472 comparison in blood TH levels across species with their life histories can provide valuable
473 information and to our knowledge, no such studies have been done. Interestingly, one study in two
474 closely-related skylark species, for example, did show that the migratory Eurasian skylarks (*Alauda*
475 *arvensis*) have higher pre-breeding blood T3 levels than the resident Asian short-toed larks
476 (*Calandrella cheleensis*, Zhao et al. 2017). If in general migratory species keep comparatively higher
477 circulating TH levels than resident species, the higher maternal TH deposition could be a reflection.
478 A meta-analysis making use of the available data from the literature should be promising to test the
479 associations between life-history variation and TH physiology.
480 Even if maternal THs are a physiological consequence brought by different life histories,
481 differential yolk TH deposition may still reinforce the evolution of the life-history variation. Due to
482 the indispensability for embryonic development, maternal THs likely have short-term and long-term
483 effects on offspring phenotype, such as nestling development, growth, and physiology (Ruuskanen
484 et al. 2016a; Hsu et al. 2017, 2019a). If higher maternal THs would lend beneficial effects for a
485 certain life-history strategy, and physiologically such a life history results in a higher maternal TH
486 transfer, maternal THs and life-history differences will influence each other and undertake a co-
487 evolution process. At the moment, this is a bold speculation. However, considering that yolk T3
488 deposition has a moderate heritability (h^2 = 0.25, Ruuskanen et al. 2016c) and clear between-
489 individual difference (Hsu et al. 2019b), there might be evolutionary potential for this to happen.
490 Future studies may examine the temporal and quantitative differences in the expression patterns of

TH-related genes in embryonic brains between migratory and resident species, and between precocial and altricial species, to know if there has been fundamental differences during the early developmental stage. Another angle would be examining whether birds hatching from eggs with elevated yolk THs may deposit higher yolk THs than control birds to test if maternal TH can induce any non-genetic inheritance.

Maternal THs and environment

In terms of environmental factors, our models suggested differences in maternal yolk THs between captive and wild species, but not between terrestrial and marine-bound species.

Captive life have favoured higher maternal TH deposition

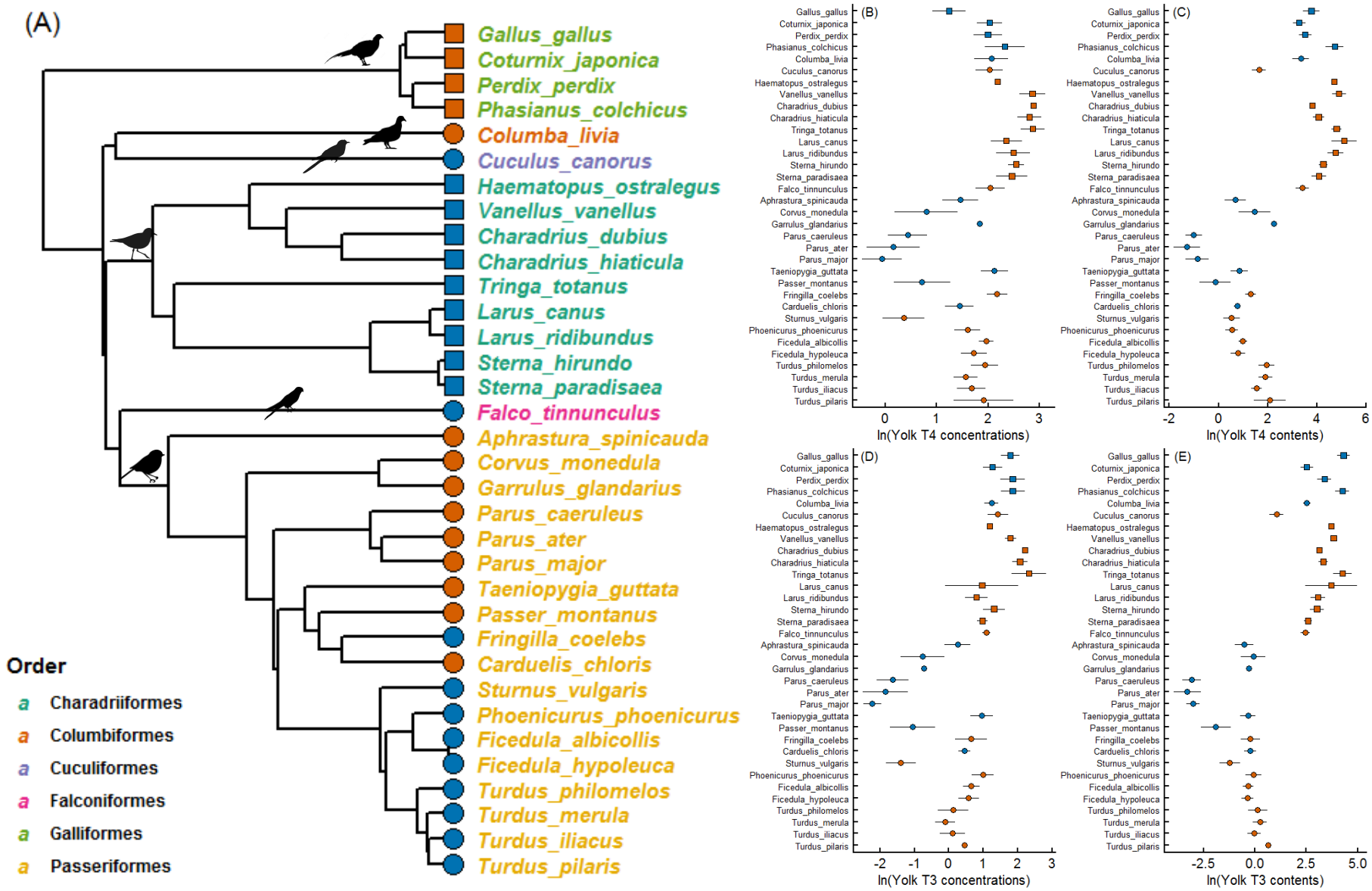
Life in captivity brings about a lot of differences, such as space confinement, (usually) unlimited food availability and free of predation (Mason 2010). Such differences from the life in the wild can influence phenotypic expression (i.e. phenotypic plasticity) and even cause selection for certain traits (Driscoll et al. 2009). For example, captive zebra finches, domesticated or not, started incubating earlier and therefore induced a stronger degree of hatching asynchrony than wild zebra finches (Gilby et al. 2013). In our study, all the captive species have acclimated to captive lives for generations. Therefore the result that captive species deposit higher levels of THs in the egg yolks likely reflects some selection under captivity. The actual selective force is elusive at the moment, but probably related to traits that are favoured in captivity, e.g. faster acclimation/habituation for anthropogenic diet or perhaps dampened stress response to confined space and constant human disturbance.

Lack of evidence for the potential link with proximity to the sea

The larger yolk TH contents in marine-bound species compared to terrestrial species, apparent from the raw data, were not supported by the phylogenetic mixed models. The most likely explanation to

517 this discrepancy is probably that all sampled marine-bound species are from the order
518 Charadriiformes, hence we lack of power to statistically partition the effects of environment and
519 phylogeny. Future studies should therefore broaden the sampling scheme to overcome this
520 problem. An alternative to test the relationship between foraging environment and maternal THs is
521 to focus on a smaller clade, such as a single order or a single species inhabiting both inland and
522 marine-bound populations. In the present study, the eggs of the little ringed plover (*Charadrius*
523 *dubius*) was sampled from an inland population. The species, interestingly, had the lowest T4
524 content among all Charadriiform species, which implies possible influence from the environment.
525 Experimentally manipulating diet iodine content in a captive model system or supplementing iodine-
526 rich food to a wild population would be also an effective approach in this respect.
527
528 Conclusion
529 In our unique data set, we measured maternal yolk T3 and T4 from 34 bird species across 6 orders
530 and analysed their associations with a large set of life-history variables when taking some
531 environmental factors into account. Our phylogenetic mixed models suggested that migratory
532 species deposited higher levels of both THs in the egg yolks than resident species, and precocial
533 species deposited higher total content of T3 in the egg yolks than altricial species. In addition,
534 captive species also consistently deposited higher levels of yolk THs, suggesting some selection
535 process under captivity. These identified patterns suggest that maternal THs may be involved in the
536 process of life-history evolution and can respond to on-going selective forces. Further effort should
537 be invested to uncover the underlying evolutionary mechanisms.
538
539 **Acknowledgement**
540 We thank Jon Brommer for his kind and helpful statistical advice in the beginning stage of data
541 analysis. We thank Jorma Nurmi for excellent nest-finding skills and effort in the field. This study was
542 funded by a grant from the Academy of Finland to SR (grant no. XXXXXX).

543

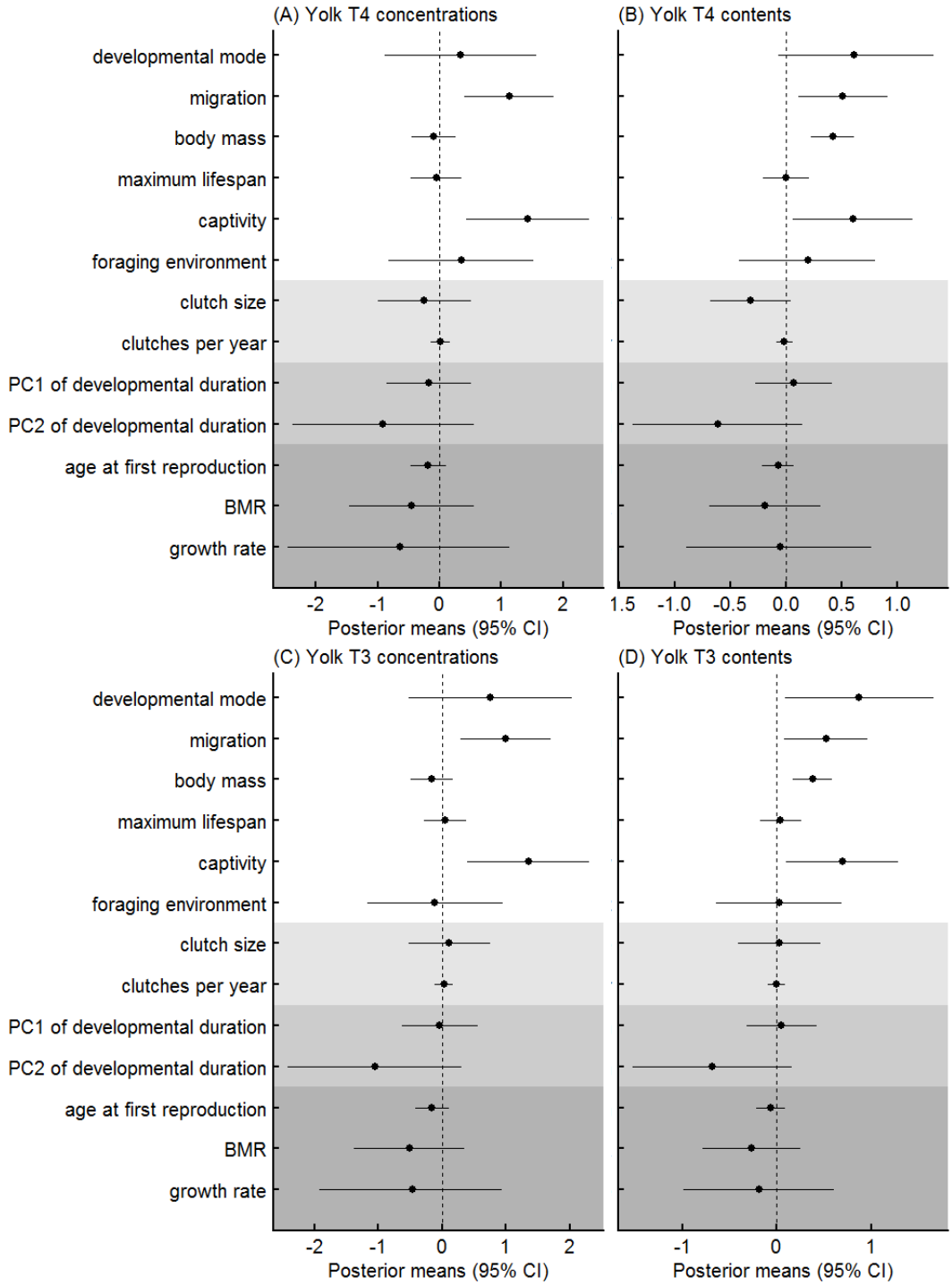

(A)
Gallus_gallus
Coturnix_japonica
Perdix_perdix
Phasianus_colchicus
Columba_livia
Cuculus_canorus
Haematopus_ostralegus
Vanellus_vanellus
Charadrius_dubius
Charadrius_hiaticula
Tringa_totanus
Larus_canus
Larus_ridibundus
Sterna_hirundo
Sterna_paradisaea
Falco_tinnunculus
Aphrastura_spinicauda
Corvus_monedula
Garrulus_glandarius
Parus_caeruleus
Parus_ater
Parus_major
Taeniopygia_guttata
Passer_montanus
Fringilla_coelebs
Carduelis_chloris
Sturnus_vulgaris
Phoenicurus_phoenicurus
Ficedula_albicollis
Ficedula_hypoleuca
Turdus_philomelos
Turdus_merula
Turdus_iliacus
Turdus_pilaris
Order
Charadriiformes
Columbiformes
Cuculiformes
Falconiformes
Galliformes
Passeriformes
(B)
ln(Yolk T4 concentrations)
(C)
ln(Yolk T4 contents)
(D)
ln(Yolk T3 concentrations)
(E)
ln(Yolk T3 contents)

544 **Figure 1.** Phylogenetic tree and yolk TH concentrations and total contents of the avian species included in this study. The phylogenetic tree (A) is one

545 possible tree derived from the Hackett backbone (see text). Different colours in species names represent different orders they belong to. Yolk TH

546 concentrations (B, D) and total contents (C, E) exhibited substantial inter-specific variation (mean±SD, see Table S1 for exact values and sample sizes). Red

547 symbols represent resident species, while blue symbols migratory species. Circles represent altricial species, and squares precocial species.



548 **Figure 2.** Posterior means (± 95% credible intervals) between yolk THs and all life-history variables
549 tested in this study. White area presents the estimates from model set 1 (see text and Table 1). The
550 shaded areas present the variables tested in model set 2 (the light and medium grey areas) and
551 model set 3-5 (the darkest grey area). In model 2-5, the estimates of the variables that had been
552 tested in model set 1 were not redundantly presented. For developmental model, the estimate
553 represents the difference of yolk THs in precocial species from altricial species. For migration, the

554 estimate represents the difference in migratory species from resident species. For captivity, the

555 estimate represents the difference in captive species from wild species. For foraging environment,

556 the estimate represents the difference in marine-bound species from terrestrial species.

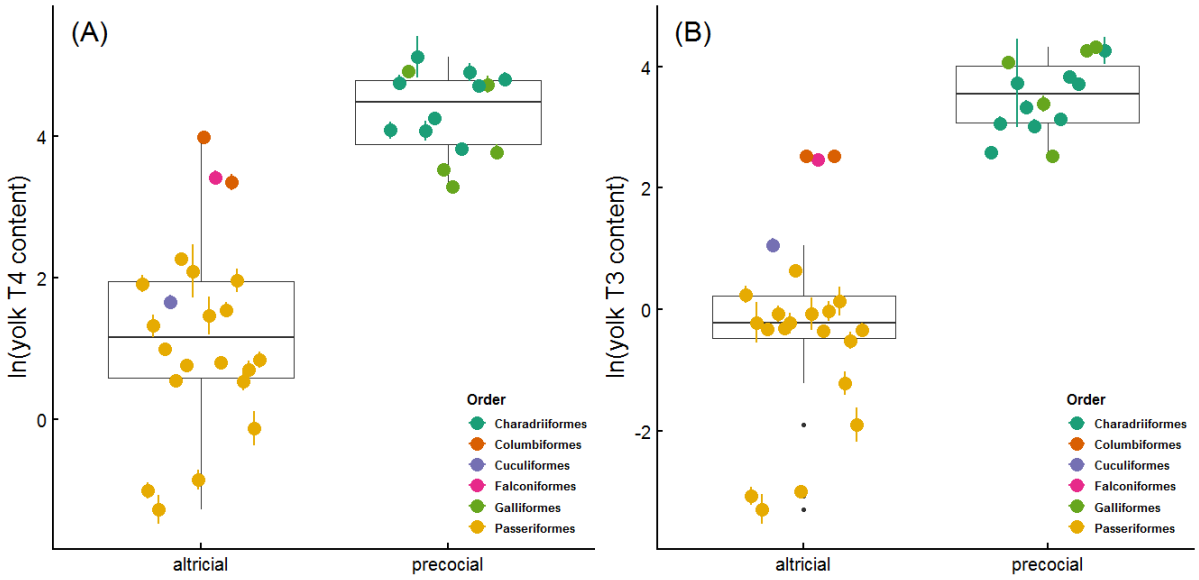


Figure 3. Boxplots and species-specific averages of yolk T4 (A) and T3 (B) contents (ng/yolk, ln-transformed raw data) according to developmental mode. Boxplots represent the median (the middle line) and the first and the third quartiles (the box), and the whiskers extend to 1.5 times of the interquartile range. Colored dots represent species-specific means (±SE).

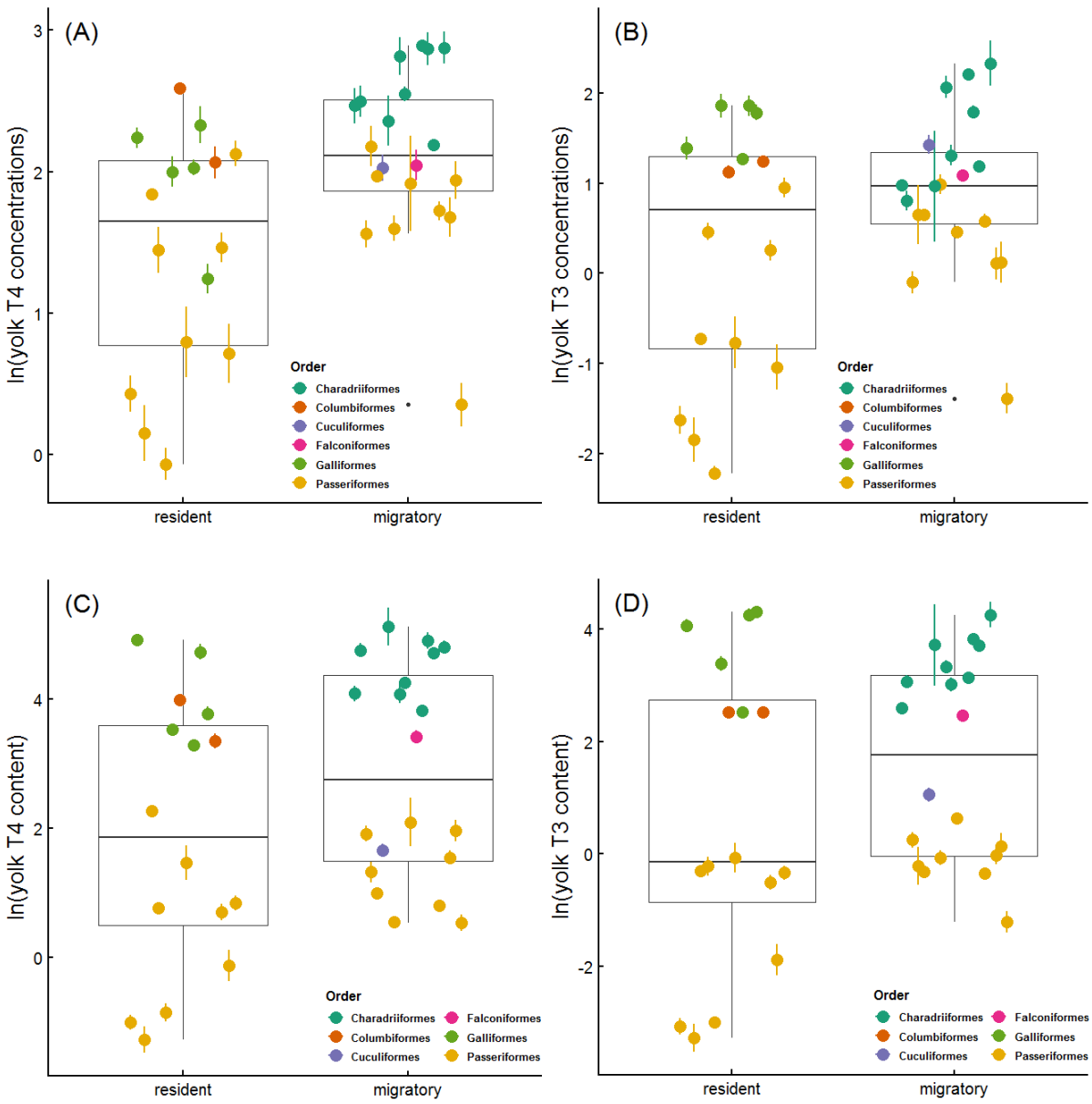
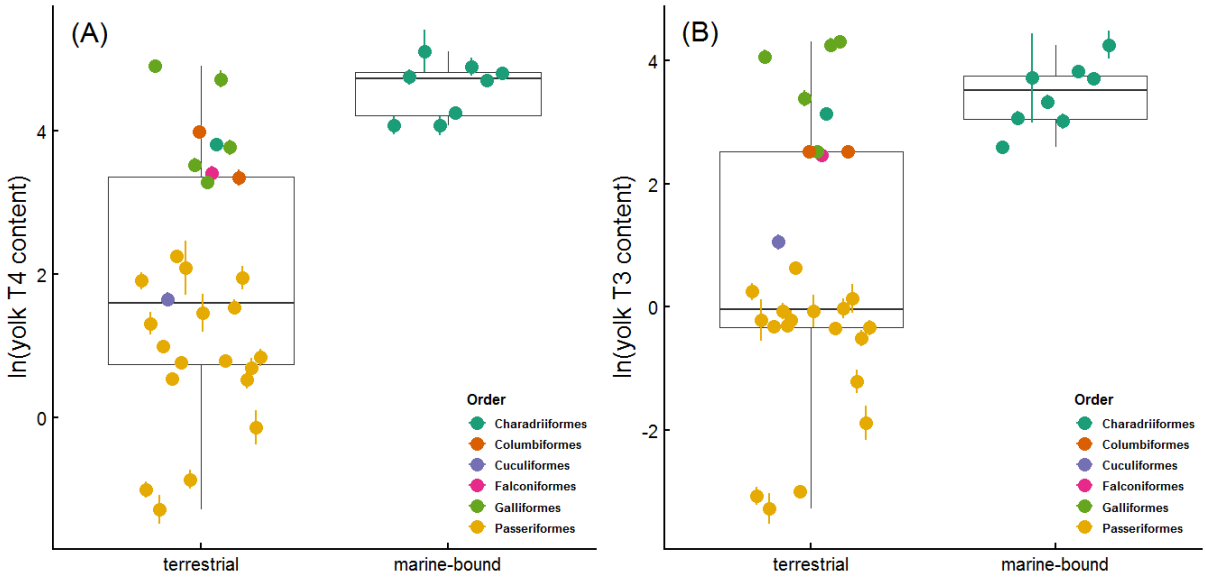


Figure 4. Boxplots and species-specific averages of yolk TH concentrations (A, B, pg/mg, ln-transformed raw data) and total contents (C, D, ng/yolk, ln-transformed raw data) between migratory and resident species. Boxplots represent the median (the middle line) and the first and the third quartiles (the box), and the whiskers extend to 1.5 times of the interquartile range. Colored dots represent species-specific means (±SE).



568

569 **Figure 5.** Boxplots of yolk T4 (A) and T3 (B) contents (ng/yolk, ln-transformed raw data) between

570 marine-bound and terrestrial species. Boxplots represent the median (the middle line) and the first

571 and the third quartiles (the box), and the whiskers extend to 1.5 times of the interquartile range.

572 Colored dots represent species-specific means (±SE).

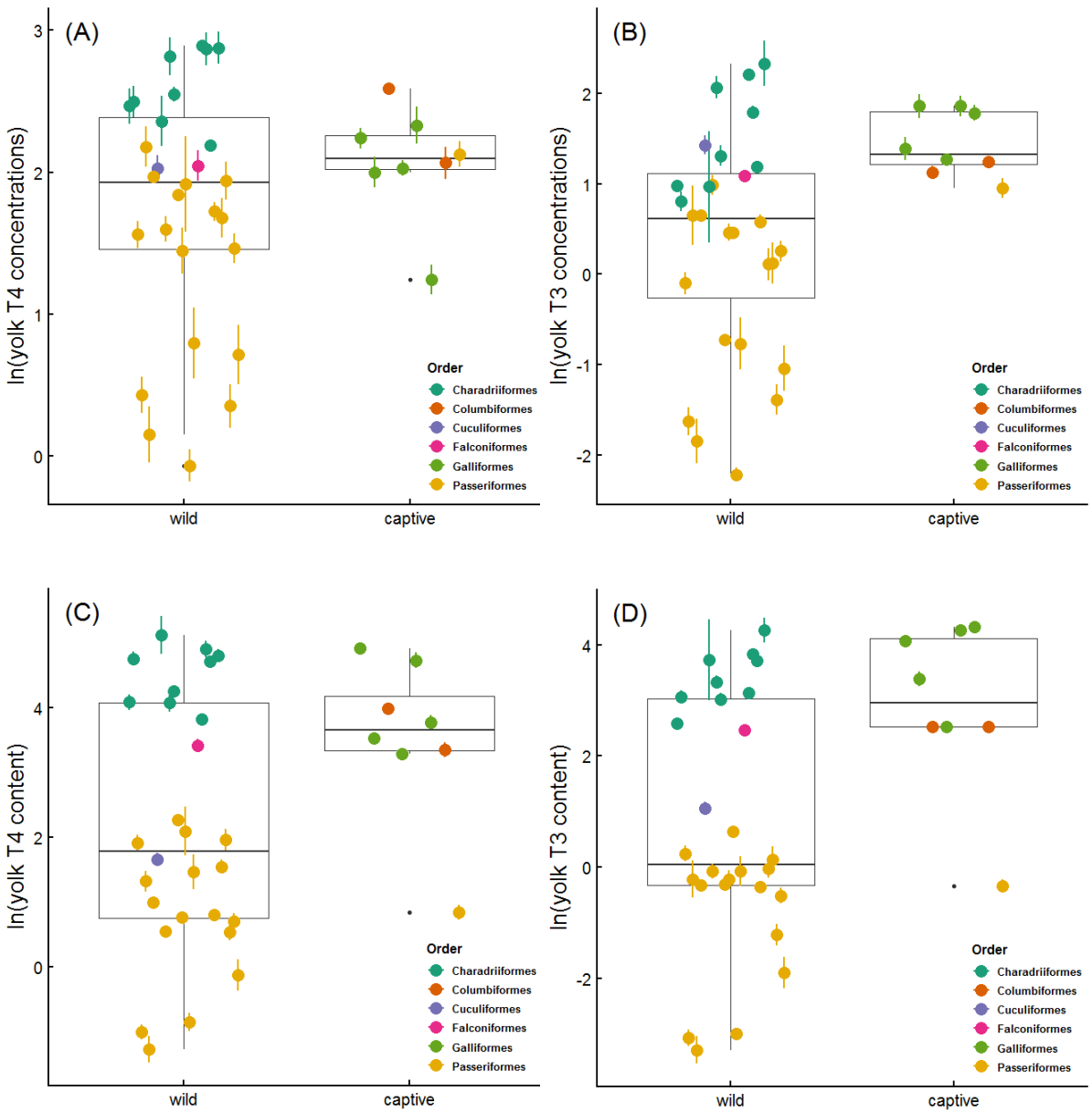


Figure 6. Boxplots of yolk TH concentrations (A, B, pg/mg, ln-transformed raw data) and total contents (ng/yolk, ln-transformed raw data) in between captive and wild species. Boxplots represent the median (the middle line) and the first and the third quartiles (the box), and the whiskers extend to 1.5 times of the interquartile range. Colored dots represent species-specific means (±SE).

578 **References**

579 Angelier, F., Parenteau, C., Ruault, S., Angelier, N. (2016). Endocrine consequences of an acute stress
580 under different thermal conditions: a study of corticosterone, prolactin, and thyroid hormones in the
581 pigeon (*Columba livia*). *Comp. Biochem. Physiol. A,* 196, 38-45.

582 Auer, S.K., Dick, C.A., Metcalfe, N.B., Reznick, D.N. (2018). Metabolic rate evolves rapidly and in
583 parallel with the pace of life history. *Nat. Commun.,* 9, 14

584 Bath, S.C, Steer, C.D., Golding, J., Emmett, P., Rayman, M.P. (2013). Effects of inadequate iodine
585 status in UK pregnant women on cognitive outcomes in their children: results from the Avon
586 Longitudinal Study of Parents and Children (ALSPAC). *Lancet,* 382, 331-337.

587 Bentley, G.E., Tucker, S., Chou, H., Hau, M., Perfito, N. (2013). Testicular growth and regression are
588 not correlated with Dio2 expression in a wild male songbird, *Sturnus vulgaris*, exposed to natural
589 changes in photoperiod. *Endocrinology*, 154, 1813-1819.

590 Bizhanova, A., Kopp, P. (2009). Minireview: the sodium-iodide symporter NIS and pendrin in iodide
591 homeostasis of the thyroid. *Endocrinology*, 150, 1084-1090.

592 Boggs, A.S.P., Hamlin, H.J., Lowers, R.H., Guillette, L.J. Jr. (2011). Seasonal variation in plasma thyroid
593 hormone concentration in coastal versus inland populations of juvenile American alligators (*Alligator*
594 *mississippiensis*): influence of plasma iodide concentrations. *Gen. Comp. Endocrinol.,* 174: 362-369.

595 Chastel, O., Lacroix, A., Kersten, M. (2003). Pre-breeding energy requirements: thyroid hormone,
596 metabolism and the timing of reproduction in house sparrows *Passer domesticus*. *J. Avian Biol.,* 34,
597 298-306.

598 Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan, B.L. et al. (2018).
599 The eBird/Clements checklist of birds of the world: v2018. Downloaded from
600 http://www.birds.cornell.edu/clementschecklist/download/

601 Cortés, D.C.C., Langlois, V.S., Fernandino, J.I. (2014). Crossover of the hypothalamic pituitary-
602 adrenal/interrenal-thyroid, and –gonadal axes in testicular development. *Front. Endocrinol.,* 5, 139.

603 Dammhahn, M., Dingemanse, N.J., Niemelä, P.T., Réale, D. (2018). Pace-of-life syndormes: a
604 framework for the adaptive integration of behaviour, physiology and life history. *Behav. Ecol.*
605 *Sociobiol.,* 72: 62.
606 Dardente, H., Hazlerigg, D.G., Ebling, F.J.P. (2014). Thyroid hormone and seasonal rhythmicity. *Front.*
607 *Endocrinol.,* 5, 19.
608 Darras, V.M. (2019). The role of maternal thyroid hormones in avian embryonic development. *Front.*
609 *Endocrinol.,* 10, 66.
610 Darras, V.M., Kotanen, S.P., Geris, K.L., Berghman, L.R., Kühn, E.R. (1996). Plasma thyroid hormone
611 levels and iodothyronine deiodinase activity following an acute glucocorticoid challenge in
612 embryonic compared with posthatch chickens. *Gen. Comp. Endocrinol.,* 104, 203-212.
613 de Groef, B., Grommer, S.V.H., Darras, V.M. (2013). Hatching the cleidoic egg: the role of thyroid
614 hormone. *Front. Endocrinol.*, 4, 63.
615 Driscoll, C.A., Macdonald, D.W., O'Brien, S.J. (2009). From wild animals to domesticated pets, an
616 evolutionary view of domestication. *Proc. Natl. Acad. Sci. U.S.A.*, 106, 9971-9978.
617 Eckhoff, K.M., Maage, A. (1997). Iodine content in fish and other food products from east Africa
618 analyzed by ICP-MS. *J. Food Compost. Anal.*, 10, 270-282.
619 Elliott, K.H., Welcker, J., Gaston, A.J., Hatch, S.A., Palace, V., Hare, J.F. *et al.* (2013). Thyroid
620 hormones correlate with resting metabolic rate, not daily energy expenditure, in two charadriiform
621 seabirds. *Biol. Open,* 2, 580-586.
622 Ericson, P.G.P., Zuccon, D., Ohlson, J.I., Johansson, U.S., Alvarenga, H., Prum, R.O. (2006). Higher-
623 level phylogeny and morphological evolution of tyrant flycatchers, cotingas, manakins, and their
624 allies (Aves: Tyrannida). *Mol. Phylogenet. Evol.,* 40, 471-483.
625 Gilby, A.J., Mainwaring, M.C., Griffith, S.C. (2013). Incubation behaviour and hatching synchrony
626 differ in wild and captive populations of the zebra finch. *Anim. Behav.*, 85, 1329-1334.
627 Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J. *et al.* (2008). A
628 phylogenomic study of birds reveals their evolutionary history. *Science,* 320, 1763-1768.

Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.,* 33, 1-22.

Hadfield, J.D., Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J. Evol. Biol.,* 23, 494-508.

Hahn, T.P., Brazeal, K.R., Schultz, E.M., Chmura, H.E., Cornelius, J.M., Watts, H.E. *et al.* (2015). Annual schedules. In: *Sturkie's Avian Physiology*, 6th edition. (ed. C.G. Scanes). Elsevier Inc., pp. 847-867.

Hau, M., Ricklefs, R.E., Wikelski, M., Lee, K.A., Brawn, J.D. (2010). Corticosterone, testosterone and life-history strategies of birds. *Proc. R. Soc. B,* 277, 3203-3212.

Houslay, T.M., Wilson, A.J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behav. Ecol.,* 28, 948-952.

Hsu, B.-Y., Dijkstra, C., Darras, V.M., de Vries, B., Groothuis, T.G.G. (2016). Maternal adjustment of constraint: differential effects of food availability on maternal deposition of macro-nutrients, steroids and thyroid hormones in rock pigeon eggs. *Ecol. Evol.,* 6, 397-411.

Hsu, B.-Y., Dijkstra, C., Darras, V.M., de Vries, B., Groothuis, T.G.G. (2017). Maternal thyroid hormones enhance hatching success but decrease nestling body mass in the rock pigeon (*Columba livia*). *Gen. Comp. Endocrinol.* 240: 174-181.

Hsu, B.-Y., Doligez, B., Gustafsson, L., Ruuskanen, S. (2019a). Transient growth-enhancing effects of elevated maternal thyroid hormones at no apparent oxidative cost during early postnatal period. *J. Avian Biol.,* 50: e01919.

Hsu, B.-Y., Verhagen, I., Gienapp, P., Darras, V.M., Visser, M.E., Ruuskanen, S. (2019b). Between- and within-individual variation of maternal thyroid hormone deposition in wild great tits (*Parus major*). *Am. Nat.,* 194, E96-E108.

Jetz, W., Thomas, G.H.,Joy, J.B., Hartmann, K., Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature,* 491, 444-448.

654 Korevaar, T.I., Muetzel, R., Medici, M., Chaker, L., Jaddoe, V.W.V., de Rijke, Y.B. *et al.* (2016).
655 Association of maternal thyroid function during early pregnancy with offspring IQ and brain
656 morphology in childhood: a population-based prospective cohort study. *Lacet Diabetes Endocrinol.,*
657 4. 35-43.
658 Kulkami, S.S., Buchholz, D.R. (2012). Beyond synergy: corticosterone and thyroid hormone have
659 numerous interaction effects on gene regulation in *Xenopus tropicalis* tadpoles. *Endocrinology,* 153,
660 5309-5324.
661 Lehikoinen, E., Gustafsson, E., Aalto, T., Alho, P., Klemola, H., Laine, J. *et al.* (2003). *Vasinais-Suomen*
662 *Linnut.* Turun Lintutieteellinen Yhdistys, Turku. (In Finnish)
663 Lehoczki, R., Erdélyi, K., Sonkoly, K., Szemethy, L., Csányi. (2011). Iodine distribution in the
664 environment as a limiting factor for roe deer antler development. *Biol. Trace Elem. Res.*, 139, 168-
665 176.
666 MacLean, B., Tomazela, D.M., Shulman, N., Chambers, M., Finney, G.L., Frewen, B. *et al.* (2010).
667 Skyline: an open source document editor for creating and analyzing targeted proteomics
668 experiments. *Bioinformatics,* 26, 966-968.
669 Mason, G.J. (2010). Species differences in responses to captivity: stress, welfare and the comparative
670 method. *Trends Ecol. Evol.*, 25, 713-721.
671 McKechnie, A.E., Freckleton, R.P., Jetz, W. (2006). Phenotypic plasticity in the scaling of avian basal
672 metabolic rate. *Proc. R. Soc. B,* 273, 931-937.
673 McNab, B.K. (2009). Ecological factors affect the level and scaling of avian BMR. *Comp. Biochem.*
674 *Physiol. A,* 152, 22-45.
675 McNabb, F.M.A. (2006). Avian thyroid development and adaptive plasticity. *Gen. Comp. Endocrinol.,*
676 147, 93-101.
677 McNabb, F.M.A., Darras, V.M. (2015). Thyroids. In: *Sturkie's Avian Physiology*, 6th edition. (ed. C.G.
678 Scanes). Elsevier Inc., pp. 535-547.

679 Medici, M., Timmermans, S., Visser, W., de Muinck Keizer-Schrama, S.M.P.F., Jaddoe, V.W.W.,
680 Hofman, A. *et al.* (2013). Maternal thyroid hormone parameters during early pregnancy and birth
681 weight: the generation R study. *J. Clin. Endocrinol. Metab.,* 98, 59-66.
682 Moog, N.K., Entringer, S., Heim, C., Wadhwa, P.D., Kathmann, N., Buss, C. (2017). Influence of
683 maternal thyroid hormones during gestation on fetal brain development. *Neuroscience, 342,* 68-100.
684 Moore, M.P., Whiteman, H.H., Martin, R.A. (2019). A mother's legacy: the strength of maternal
685 effects in animal populations. *Ecol. Lett.*, 22, 1620-1628.
686 Mousseau, T.A., Fox, C.W. (1998). *Maternal effects as adaptations.* Oxford University Press, New
687 York, NY.
688 Mullur, R., Liu, Y.-Y., Brent, G.A. (2014). Thyroid hormone regulation of metabolism. *Physiol. Rev.,* 94,
689 355-382.
690 Myhrvold, N.P., Baldridge, E., Chan, B., Sivam, D., Freeman, D.L., Ernest, S.K.M. (2015). An amniote
691 life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology,*
692 96, 3109.
693 Nakao, N., Ono, H., Yamamura, T., Anraku, T., Takagi, T., Higashi, K. *et al.* (2008). Thyrotrophin in the
694 pars tuberalis triggers photoperiodic response. *Nature*, 452, 317-323.
695 Nishiwaki-Ohkawa, T., Yoshimura, T. (2016). Molecular basis for regulating seasonal reproduction in
696 vertebrates. *J. Endocrinol.,* 229, R117-R127.
697 Pap, P.L., Vágási, C.I., Vincze, O., Osváth, G., Veres-Szászka, J., Czirják, G.Á. (2015). Physiological pace
698 of life: the link between constitutive immunity, developmental period, and metabolic rate in
699 European birds. *Oecologia,* 177, 147-158.
700 Perfito, N., Jeong, S.Y., Silverin, B., Calisi, R.M., Bentley, G.E., Hau, M. (2012). Anticipating spring: wild
701 populations of great tits (*Parus major*) differ in expression of key genes for photoperiodic time
702 measurement. *PLoS ONE*, 7, e34997.
703 Pérez, J.H., Furlow, J.D., Wingfield, J.C., Ramenofsky, M. (2016). Regulation of vernal migration in
704 Gambel's white-crowned sparrows: role of thyroxine and triiodothyronine. *Horm. Behav.,* 84, 50-56.

Pérez, J.H., Meddle, S.L., Wingfield, J.C., Ramenofsky, M. (2018). Effects of thyroid hormone manipulation on pre-nuptial molt, luteninzing hormone and testicular growth in male white-crowned sparrows (*Zonotrichia leuchophrys gambelii*). *Gen. Comp. Endocrinol.,* 255: 12-18.

Plummer, M., Best, N., Cowles, K., Vines, K. (2006). CODA: convergence diagnosis and output analysis for MCMC. *R News,* 6, 7-11.

Prati, M., Calvo, R., Morreale de Escobar, G. (1992). L-thyroxine and 3,5,3'-triiodothyronine concentrations in the chicken egg and in the embryo before and after the onset of thyroid function. *Endocrinology,* 130, 2651-2659.

Price, E.R., Dzialowski, E.M. (2018). Development of endothermy in birds: patterns and mechanisms. *J. Comp. Physiol. B*, 188, 373-391.

Revell, L.J. (2009). Size-correction and principal components for interspecific comparative studies. *Evolution,* 63, 3258-3268.

Revell, L.J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.,* 3, 217-223.

Ricklefs, R.E., Wikelski, M. (2002). The physiology/life-history nexus. *Trends Ecol. Evol.,* 17, 462-468.

Rubolini, D., Liker, A., Garamszegi, L.Z., Møller, A.P., Saino, N. (2015). Using the BirdTree.org website to obtain robust phylogenies for avian comparative studies: a primer. *Curr. Zool.,* 61, 959-965.

Ruuskanen, S., Hsu, B.-Y. (2018). Maternal thyroid hormones: an unexplored mechanism underlyinbg maternal effects in an ecological framework. *Physiol. Biochem. Zool.,* 91, 904-916.

Ruuskanen, S., Darras, V.M., Visser, M.E., Groothuis, T.G.G. (2016a). Effects of experimentally manipulated yolk thyroid hormone levels on offspring development in a wild bird species. *Horm. Behav.,* 81: 38-44.

Ruuskanen, S., Darras, V.M., de Vries, B., Visser, M.E., Groothuis, T.G.G. (2016b). Experimental manipulation of food availability leads to short-term intra-clutch adjustment in egg mass but not in yolk androgen or thyroid hormones. *J. Avian Biol.,* 47: 36-46.

730 Ruuskanen, S., Gienapp, P., Groothuis, T.G.G., Schaper, S.V., Darras, V.M., Pereira, C. *et al.* (2016c).
731 Heritable variation in maternally derived yolk androgens, thyroid hormones, and immune factors.
732 *Heredity,* 117, 184-190.
733 Ruuskanen, S., Hsu, B.-Y., Heinonen, A., Vainio, M., Darras, V.M., Sarraude, T. *et al.* (2018). A new
734 method for measuring thyroid hormones using nano-LC-MS/MS. *J. Chromatogr. B,* 1093-1094, 24-30.
735 Sechman, A., Bobek, S. (1988). Presence of iodothyronines in the yolk of the hen's egg. *Gen. Comp.*
736 *Endoccrinol.,* 69, 99-105.
737 Starck, J.M., Ricklefs, R.E. (1998a). Patterns of development: the altricial-precocial spectrum. In:
738 *Avian Growth and Development: Evolution within the Altricial-Precocial Spectcrum*. (eds. Starck, J.M.,
739 Ricklefs, R.E.) Oxford University Press, New York, NY, pp. 3-30.
740 Starck, J.M., Ricklefs, R.E. (1998b). Avian growth rate data set. In: *Avian Growth and Development:*
741 *Evolution within the Altricial-Precocial Spectcrum*. (eds. Starck, J.M., Ricklefs, R.E.) Oxford University
742 Press, New York, NY, pp. 381-415.
743 Starck, J.M., Ricklefs, R.E. (1998c). *Avian Growth and Development: Evolution within the Altricial-*
744 *Precocial Spectrum*. Oxford University Press, New York, NY.
745 Tacutu, R., Craig, T., Budovsky, A., Wuttke, D., Lehmann, G., Taranukha, D. *et al.* (2013). Human
746 ageing genomic resources: Integrated databases and tools for the biology and genetics of ageing.
747 *Nucleic Acids Res.,* 41, D1027-D1033.
748 Tomasek, O., Bobek, L., Kralova, T., Adamkova, M., Albrecht, T. (2019). Fuel for the pace of life:
749 baseline blood glucose concentration co-evolves with life-history traits in songbirds. *Funct. Ecol.,* 33,
750 239-249.
751 Trumpff, C., de Schepper, J., Tafforeau, J., van Oyen, H., Vanderfaeillie, J., Vandervijvere, S. (2013).
752 Mild iodine deficiency in pregnancy in Europé and its consequences for cognitive and psychomotor
753 development of children: a review. *J. Trace Elem. Med. Biol.,* 27, 174-183.
754 Vágási, C.I., Vincze, O., Pătraş, L., Osváth, G., Pénzes, J., Haussmann, M.F. *et al.* (2019). Longevity and
755 life history coevolve with oxidative stress in birds. *Funct. Ecol.,* 33, 152-161.

van Herck, S.L.J., Geysens, S., Delbaere, J., Tylzanowski, P. Darras, V.M. (2012). Expression profile and thyroid hormone responsiveness of transporters and deiodinases in early embryonic chicken brain development. *Mol. Cell. Endocrinol.*, 349, 289-297.

Vézina, F., Gustowska, A., Jalvingh, K.M., Chastel, O., Piersma, T. (2009). Hormonal correlates and thermoregulatory consequences of molting on metabolic rate in a northerly wintering shorebird. *Physiol. Biochem. Zool.,* 82, 129-142.

Villanueva, I., Alva-Sánchez, C., Pacheco-Rosado, J. (2013). The role of thyroid hormones as inductors of oxidative stress and neurodegeneration. *Oxid. Med. Cell. Longev.* 2013, 218145.

Wada, H. (2008). Glucocorticoids: mediators of vertebrate ontogenetic transistions. *Gen. Comp. Endocrinol.*, 156, 441-453.

Welcker, J., Chastel, O., Gabrielsen, G.W., Guillaumin, J., Kitaysky, A.S., Speakman, J.R. *et al.* (2013). Thyroid hormones correlate with basal metabolic rate but not field metabolic rate in a wild bird species. *PLoS ONE,* 8, e56229.

Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A., Gwinner, E. (2003). Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proc. R Soc. Lond. B,* 270, 2383-2388.

Zhao, L., Gao, L., Yang, W., Xu, X., Wang, W., Liang, W. *et al.* (2017). Do migrant and resident species differ in the timing of increases in reproductive and thyroid hormone secretion and body mass? A case study in the comparison of pre-breeding physiology rhythms in the Eurasian skylark and Asian short-toed lark. *Avian Res.*, 8, 10.

776 **Supplementary materials**

777 The compiled data set and literature sources we consulted will be provided as additional

778 supplementary materials or deposited in a public repository upon final publication.

779

780 **Table S1.** Mean±SD of yolk T3 and T4 concentrations and total contents of all 34 species in this

781 study.

Species	N of T3	Yolk T3 concentration (pg/mg yolk)	Yolk T3 content (ng/yolk)	N of T4	Yolk T4 concentration (pg/mg yolk)	Yolk T4 content (ng/yolk)
Japanese quail, *Coturnix japonica*	21	3.690±1.009	13.035±3.787	21	7.802±1.661	27.514±6.846
Red jungle fowl, *Gallus gallus gallus*	10	6.163±1.852	78.122±25.792	10	3.633±1.215	45.991±16.501
Domesticated chicken, *Gallus gallus domesticus*	5	4.151±1.315	59.809±16.053	5	9.488±1.621	137.149±16.649
Grey partridge, *Perdix perdix*	7	6.803±2.765	31.229±12.491	7	7.633±2.159	34.930±9.072
Ringed-necked pheasant, *Phasianus colchicus*	9	6.743±2.010	74.055±22.609	9	11.060±5.022	120.725±52.997
Common cuckoo, *Cuculus canorus*	8	4.322±1.065	2.998±0.788	8	7.821±2.112	5.397±1.462
Rock pigeon, *Columba livia livia*	9	3.532±0.785	12.685±2.351	9	8.303±2.982	29.978±10.289
Homing pigeon, *Columba livia domesticus*	4	3.103±0.463	12.575±2.084	4	13.339±0.687	53.981±3.341
Eurasian oystercatcher, *Haematopus ostralegus*	1	3.285	40.782	1	8.946	111.068
Northern Lapwing, *Vanellus vanellus*	5	6.051±0.942	46.195±6.027	5	18.050±4.497	139.166±39.438
Little ringed plover, *Charadrius dubius*	1	9.098	22.972	1	17.984	45.409
Common ringed plover, *Charadrius hiaticula*	3	8.021±1.630	28.325±5.727	3	16.965±3.871	59.980±14.134
Redshank, *Tringa tetanus*	4	11.242±5.067	76.245±32.722	4	18.101±4.125	123.911±25.503
Common tern, *Sterna hirundo*	8	3.883±1.250	21.563±7.313	8	12.920±1.844	71.466±11.647
Arctic tern, *Sterna paradisaea*	6	2.681±0.429	13.602±2.926	6	12.229±3.479	61.544±17.678
Common gull, *Larus canus*	3	3.723±3.521	67.738±75.481	3	10.929±3.444	182.853±99.314
Black-headed gull, *Larus ribidundus**	9	2.363±0.883	22.773±9.292	9	12.789±4.801	121.907±43.035
Kestrel, *Falco tinnunculus*	7	3.000±0.356	12.001±2.698	7	7.992±2.238	31.472±9.262
Thorn-tailed rayadito, *Aphrastura spinicauda*	11	1.375±0.503	0.656±0.278	11	4.564±1.647	2.192±0.996
Jackdaw, *Corvus monedula*	5	0.552±0.390	1.079±0.703	6	2.529±1.248	4.982±2.464

Eurasian jay, *Garrulus glandarius*	1	0.485	0.739	1	6.287	9.568
Blue tit, *Parus caeruleus**	9	0.217±0.104	0.051±0.024	9	1.647±0.659	0.385±0.134
Great tit, *Parus major*	11	0.112±0.032	0.053±0.020	12	0.989±0.292	0.458±0.162
Coal tit, *Parus ater**	7	0.186±0.106	0.045±0.027	7	1.301±0.619	0.312±0.157
Zebra finch, *Taeniopygia guttata*	9	2.729±1.084	0.767±0.372	9	8.681±2.733	2.462±1.028
Tree sparrow, *Passer montanus*	7	0.415±0.232	0.187±0.127	7	2.294±1.046	1.015±0.510
Chaffinch, *Fringilla coelebs*	2	2.016±0.896	0.853±0.391	2	8.927±1.798	3.768±0.815
Greenfinch, *Carduelis chloris**	3	1.603±0.285	0.826±0.244	3	4.366±1.276	2.160±0.273
European starling, *Sturnus vulgaris*	7	0.273±0.131	0.334±0.179	7	1.537±0.695	1.794±0.670
Common redstart, *Phoenicurus phoenicurus*	8	2.805±0.850	0.998±0.367	8	5.073±1.151	1.774±0.424
Collared flycatcher, *Ficedula albicollis*	15	1.978±0.489	0.753±0.201	15	7.209±0.998	2.737±0.418
Pied flycatcher, *Ficedula hypoleuca*	15	1.862±0.570	0.740±0.238	15	5.763±1.421	2.307±0.654
Song thrush, *Turdus philomelos*	4	1.222±0.586	1.260±0.678	4	7.157±2.045	7.389±2.607
Blackbird, *Turdus merula*	6	0.939±0.307	1.353±0.525	6	4.881±1.233	7.013±2.147
Fieldfare, *Turdus pilaris*	3	1.587±0.111	1.904±0.257	3	7.521±3.852	9.200±5.259
Redwing, *Turdus iliacus*	4	1.168±0.376	1.009±0.276	4	5.509±1.543	4.745±0.996

* In order to match the phylogenetic trees from BirdTree.org, "old" scientific names were still used in this study. Their updated scientific names according to The Clements checklist of birds of the world v2018 (Clements et al. 2018) are: Chroicocephalus *ridibundus*, *Cyanistes caeruleus, Periparus ater, Chloris chloris*

785 **Table S2.** Dummy code for the two-level categorical variables included in the phylogenetic mixed

786 models.

	-0.5	0.5
Mode of development	altricial	precocial
Migratory status	resident	migratory
Foraging environment	terrestrial	marine-bound
Captivity	wild	captive

787

788 **Table S3.** Proportion of variance explained and loadings of the phylogeny-corrected PCA among the

789 four variables of developmental duration.

	PC1	**PC2**
Proportion of variance	83.26	16.48
Cumulative proportion	83.26	99.74
Loadings		
Incubation duration	0.264	-0.965
Time to fledging	0.998	0.055
Total developmental length	0.942	-0.329
Prenatal proportion	-0.869	-0.489

790

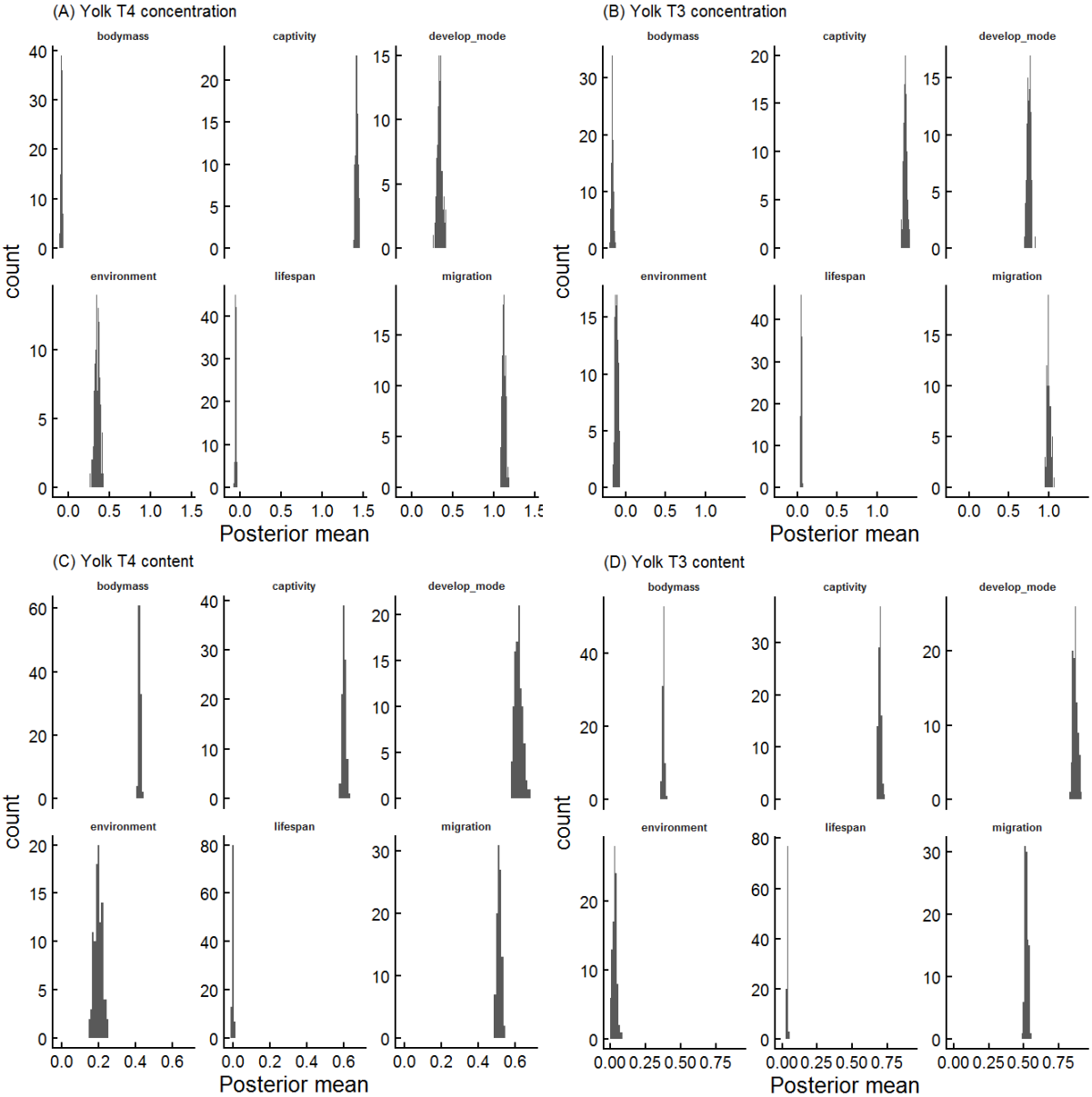
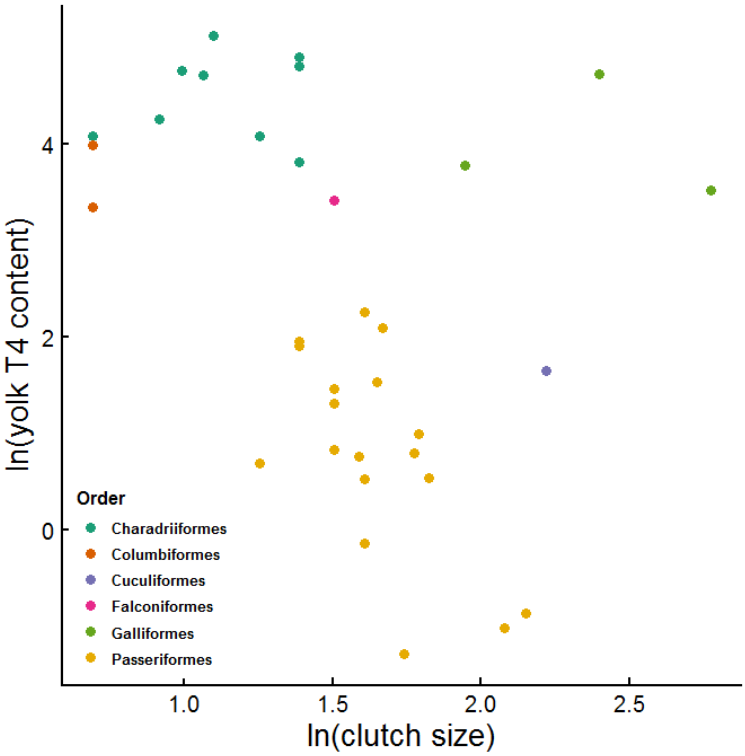


Figure S1. Histograms of posterior means for each life-history traits tested in model and data set 1 (see Table 1) across 100 possible phylogenetic trees from the Hackett backbone. All results were highly similar across different trees, indicated by the narrow range of the posterior means.



806 **Figure S2.** Scatterplot of species clutch size and yolk T4 content on a natural-log scale. Dots

807 represent species-specific means and colors represent the orders they belong to.