Fundamental constraints on the evolution of vertebrate life histories

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keywords:-body size, ecological opportunity, lifetime mortality, parity mode, viviparity

ABSTRACT

The evolution of vertebrate life histories has been fuelled by key transitions among water and land. Life history diversity evolves according to the interplay of predation on juveniles and adults, the physical properties of the environment, and the developmental context of each lineage. The selection pressures of each environment dictate which life-history strategies persist over evolutionary time and render certain strategies impossible. Despite the well-recognized shifts in selective pressures accompanying transitions among environments, the conditions driving innovation and its consequences for life-history evolution have never been comprehensively tested. Here, we show that the contrasting fitness landscapes operating in aquatic and terrestrial environments result in predictable shifts in demographic and evolutionary constraints that explain differences in vertebrate life histories. Specifically, our results emphasize the reduced potential for life-history diversification on land, especially that of reproductive strategies. Moreover, our study reveals differences between the evolution of viviparity in the two environments. Transitions from egg laying to live birth represents a major shift across life-history space for aquatic organisms, whereas terrestrial egg-laying organisms evolve live birth without drastic changes in life-history strategy. Whilst trade-offs in the allocation of resources place fundamental constraints on the way life histories can vary, ecological setting defines the macroevolutionary space that species can explore.

INTRODUCTION

The evolution of diversity of vertebrate life histories has been fuelled by key transitions among water and land, as well as a myriad of life history traits that act to modulate investment in development and reproduction. For example, the evolution of internal fertilization is a necessary but insufficient innovation to explain repeated transitions to bearing live young (viviparity) in aquatic and terrestrial environments (Blackburn 1992, Wourms and Lombardi 1992, Kalinka 2015, Vági et al. 2022). The consequences of innovations in reproduction can have cascading effects on available niche space, life histories, and macro-evolutionary patterns. Viviparity is intricately connected to parental care, egg size, and fertilization mode (Gross and Sargent 1985, Farmer 2000, Vági et al. 2019, 2022). These characteristics, in turn, can limit evolutionary lability or allow species to capitalize on novel ecological opportunities (Helmstetter et al. 2016, Reznick et al. 2021, Miller et al. 2023, Nuño de la Rosa 2023). Transitions in reproductive mode are key to the evolution of vertebrate diversity, but the consequences for life-history traits and demography could differ in aquatic and terrestrial environments.

Life history traits related to growth, reproduction, and survival determine an individual's maximum size, fitness, and pace-of-life (Stearns 1992; Roff 1992; Kindsvater et al. 2016, White et al. 2022) and provide a fundamental link between population demography and growth as well as evolutionary dynamics. Life history diversity evolves according to the interplay of predation on juveniles and adults, the physical properties of the environment, and the developmental context of each lineage (Partridge and Harvey 1988, Stearns 1992, Healy et al. 2019). The selection pressures of each environment dictate which life-history strategies persist over evolutionary time and render certain strategies impossible

(Southwood 1988), while phylogenetic inertia contributes by determining which strategies can be attained via evolution. Transitions between aquatic and terrestrial habitats have led to radiations into unexploited niches in both habitats. These transitions require key adaptations in development and reproduction that foster success in the new context. Alongside the preeminent colonization of land that marks the origin of tetrapods, transitions to an entirely terrestrial life history have evolved independently in multiple amphibian clades, accompanied by the evolution of direct development, in which juveniles complete metamorphosis prior to hatching on land. Reversions back to the water have occurred in most vertebrate clades (Colbert 1955).

The fundamental differences between species in water versus on land reflect the consequences of the unique physical and ecological features of life in water for growth, reproduction, and dispersal (Strathmann 1990, Dawson and Hamner 2008, Burgess et al. 2016, Capdevila et al. 2020). Aquatic environments prevent desiccation, buffer thermal ranges relative to the extreme temperature possible on land and offer structural support against the pull of gravity (Strathmann 1990, Dawson and Hamner 2008, Burgess et al. 2016). Additionally, aquatic food webs are more complex, and resources tend to be less patchy in space and time (though exceptions are common; Chase 2000, Weston et al. 2008, Steele et al. 2019). External fertilization is common among aquatic species, most of which release small eggs that disperse in the water column (Strathmann 1990, Burgess et al. 2016). However, the repeated evolution of internal fertilization has made the transition to viviparity possible in some ancestrally egg-laying lineages of elasmobranchs (sharks and rays), teleosts (ray finned fishes), and amphibians. A key innovation in vertebrate diversification on land was the evolution of amniotic egg, which requires internal

fertilization, and prevents desiccation of eggs in air. Several amniotic vertebrates have subsequently evolved partially or fully aquatic life histories but must lay and care for their eggs on land. A few amniotic lineages, such as some sea snakes and aquatic mammals, have escaped this constraint by evolving viviparity. Other amniotic clades including some reptiles and all birds instead produce large eggs that are protected via an eggshell, extensive parental care, or both (Martin and Carter 2013, Vági et al. 2019).

Despite the well-recognized shifts in selective pressures accompanying transitions among environments, the conditions driving developmental innovation and its consequences for life history diversity and evolutionary processes have never been comprehensively tested. One challenge is that the phylogenetic scales that hold the necessary variation for comprehensively identifying the constraints to life history variation also carry considerable variation in the traits that taxa use to modulate their life history (e.g. parity mode may be a good proxy for parental investment in many squamates, but not in amphibians). This means that finding traits that allow quantitative comparisons of across clades is challenging. Here, we used extant vertebrates, including cartilaginous fishes, bony fishes, amphibians, reptiles, birds, and mammals to demonstrate that the constraints imposed by life on land, or indeed the evolutionary release experienced when entering the water, exert a predictable shift in demographic and evolutionary constraints, with important consequences for the evolution of biodiversity. To accomplish this study, we define a novel trait space that enables comparisons of the complex, interrelated sets of trade-offs underlying all life histories with broadly available trait data, facilitating the generation of hypotheses and guiding tests of these hypotheses with macroevolutionary data. Specifically, we used proxies for life history traits where precise information is lacking to understand life history evolution throughout

111 the diversification of vertebrates. This approach improves our understanding of the
112 vertebrate invasion of land, reversions back to the water, and the evolution of live birth.

113 **METHODS**

114 ***Trait and phylogenetic data:-***A phylogeny for vertebrates was assembled on a order-level
115 backbone obtained using median divergence times from the timetree of life (Hedges et al.
116 2006). A supertree was made by grafting published trees for each clade (Figure S2). We
117 combined trees for fish (Rabosky et al. 2018), mammals (Zhou et al. 2013, Upham et al.
118 2019), birds (Jetz et al. 2012), squamates (Tonini et al. 2016), amphibians (Jetz & Pyron
119 2018), testudines (Thomson et al. 2021), crocodylians (Hedges et al. 2015), and
120 chondrichthyans (sharks, skates, rays, and chimaeras; hereafter sharks, Stein et al. 2018). As
121 the full shark phylogeny was constructed with a birth-death polytomy resolver, we chose to
122 base our analyses on the molecular backbone phylogeny calibrated with 10 fossil calibration
123 dates comprising 610 species from all major orders. The phylogeny includes both oviparous
124 and viviparous lineages and provides good coverage for the order Carcharhiniformes which
125 exhibits the greatest diversity of reproductive modes.

126 Life history traits were compiled from publicly available databases that cover the major
127 vertebrate clades. The complete dataset for all vertebrate clades used in this paper is
128 provided as supplementary material, and summarized in Table 1 (Table 1, Appendix 1). Data
129 for bony fish (Actinopterygii) were downloaded from FishBase using the rfishbase package
130 (www.fishbase.org; Froese 1992). Data for sharks and rays (Chondrichthyans) were taken
131 from the Sharkipedia data repository (www.sharkipedia.org; Mull et al. 2022). Amphibian
132 trait data were taken from AmphiBio (Oliveira et al. 2017). Data for squamate reptiles were
133 taken from Meiri et al. (2018) and supplemented with estimates of longevity sourced from

the literature. Data for birds and mammals were obtained from Myhrvold et al. (2015). We performed manual searches of the literature to bolster our dataset. We were able to source data for an additional 17 species of bony fish, 137 snakes, 137 amphibians, 45 turtles (Testudines) and 9 crocodilians. Owing to the number of species included in the analysis we had to assume that the information obtained from previously published datasets were reliable but performed post-hoc checks of influential data points as to their accuracy.

Table 1. Number of species for each of the major vertebrate clades for which life-history data was available. Numbers in parentheses are percentages of the total number of species included in each group.

Clade	Total	Internal Fertilization	Viviparity	Terrestrial Eggs	Terrestrial Adults
Chondrichthyes	115 (19%)	100%	81%	0%	0%
Actinopterygii	117 (0.05%)	17%	15%	0%	0%
Amphibia	260 (4%)	33%	3%	6%	95%
Reptilia	213 (3%)	100%	14%	100%	64%
Aves	356 (4%)	100%	0%	100%	100%
Mammalia	1465 (30%)	100%	99%	97%	94%

Body size measurements are snout-vent length (SVL) for all amphibians, reptiles, and mammals. Body sizes reported for bony fish, sharks, skates, and chimaeras represent total length, and measurements for rays reflect disc width. When multiple measurements were available for a species, mean values were used for analysis. If sex-specific estimates were available, we used numbers reported for females. Most of the trait databases did not include mass, so to convert lengths to mass we used available female length-weight (L-W) or width-weight conversion relationships. When sex and species-specific L-W relationships were unavailable we estimated reasonable L-W relationships from the same genus or family. Reproductive mode was characterized as either egg-laying or live-bearing, and fertilization mode was coded as internal or external. Species were classified as either

aquatic or terrestrial, and to account for biphasic life-cycles juveniles and adults were classified separately (e.g., most amphibians are coded as aquatic juveniles and terrestrial adults). In total, we compiled a data set including… (Figure S3, Table 1).

Our proxy for adult mortality only requires an estimate of age at maturity, such that:

$$M_a = ln(1/A_{mat})$$

where A_{mat} is the age at maturity and M_a is adult mortality (Kindsvater et al. 2018). Calculating lifetime fecundity requires information on lifespan, age at first reproduction, breeding frequency (e.g. annual, biennial) and clutch size, such that lifetime egg production is equal to:

$$M_j = ln((A_{max} - A_{mat}) * (F * b))$$

where A_{max} is longevity, A_{mat} is maturity, F is fecundity, and b represents the number of breeding bouts per year. The distribution of all three life-history traits, split between aquatic and terrestrial species, with egg-laying and live-bearing reproductive modes is presented in Figure S1. To produce a crude measure of lifetime mortality for each species, we scaled and summed our proxies of juvenile mortality and adult mortality.

$$M_{total} = scaled(M_j) + scaled(M_a)$$

where our proxies of juvenile and adult mortality are first scaled before they are summed.

Collating data on body size, age at maturity, and lifetime reproductive output allowed us to place species on common life-history axes, despite differences in ecology and traits underlying these values. We compared the distribution of body sizes, age at first reproduction, and lifetime fecundity across species, and related them to occupancy of

175 aquatic and terrestrial environments in different life stages (Figure S1). We also considered
176 whether species have internal or external fertilization and whether they are live-bearing
177 (viviparous) or egg-laying (oviparous). Our proxies were derived based on life-history theory
178 and the principle that persistence of populations and species over evolutionary timescales
179 must all fulfil the same requirement, namely that individual females, on average, must
180 replace themselves and their mate (Gadgil and Bossert 1970, Partridge and Harvey 1988,
181 Leimar 2002). Expected lifetime production of offspring is an indirect measure of juvenile
182 mortality and per offspring parental investment (Gadgil and Bossert 1970; Kindsvater et al.
183 2018). Similarly, age at first reproduction is strongly linked to adult mortality, whereby
184 species that mature later have higher survival and longer expected lifespans (Charnov 1990,
185 Charnov and Berrigan 1990). Organisms with longer lifespans therefore must, on average,
186 replace themselves at a slower rate than those with shorter lifespans; any other scenario
187 would result in the unrealistic outcomes of exponential growth or extinction. However, both
188 adult and juvenile mortality are also strongly related to body size, with larger animals often
189 exhibiting larger clutch sizes and delayed maturity (Darwin 1874, Williams 1966).
190 Fundamentally, body size represents investment that must be made in the growth and
191 metabolic maintenance of body tissues outside of direct investment in reproduction.
192 However, the consequences of transitions from water to land on species' survival and
193 growth are poorly understood.

194 ***Statistical Analyses:-***We estimated the covariances among traits using both phylogenetic
195 and non-phylogenetic estimates using multivariate Brownian Motion models of trait
196 evolution. The assumption of multivariate Brownian Motion is likely inappropriate, and
197 therefore we used an alternative phylogenetic modeling approach (see below).

198 Nevertheless, estimates of phylogenetic and non-phylogenetic correlation matrices among
199 traits is a meaningful summary statistic of the covariances among traits across the
200 observable evolutionary process. Therefore, we used a Pagel's λ model and the R package
201 *phylopars* (Goolsby et al. 2017) to accommodate for partially missing data, with analyses run
202 multiple times with species missing 0, 1, or 2 trait values excluded. Analyses were
203 performed once with a fully phylogenetic model (λ = 1) and again in a non-phylogenetic
204 model (λ = 0) to facilitate comparisons of the phylogenetic and non-phylogenetic estimates
205 with missing data.

206 To determine the relationship between maximum body size and mortality estimates, we fit
207 three separate linear regression models with juvenile mortality, adult mortality, and lifetime
208 mortality as response variables. In each model body size, habitat (aquatic or terrestrial), and
209 their interaction were included as predictors. As we were interested in the overall bounds
210 on life-history space, rather than clade-specific relationships, our primary analyses did not
211 correct for phylogeny – the uncorrected formulation is likely more informative for our
212 research question as it emphasizes the bounds of the trait space rather than the covariances
213 of changes among lineages (Simpson 1951, Reznick et al. 2000, Uyeda et al. 2018). We then
214 performed the same regressions corrected for phylogeny using the function *phylopars.lm*
215 (Goolsby et al. 2017). We assumed phylogenetically correlated residuals evolving under an
216 Ornstein-Uhlenbeck process. To quantify taxonomic heterogeneity in the relationship
217 between body size and mortality, we performed the comparative analyses separately for
218 every major clade (Figure S4). For each model we obtained average effect sizes, and their
219 associated standard errors and p-values. Model fit was evaluated by comparing predicted
220 and observed mortality values and estimating R^2 using the *rr2* package (Ives and Li 2018).

221 Ternary plots are often used for “phases” or regions of interactions that have a distinct
222 shared feature (e.g. ‘solid’, ‘liquid’ or ‘gas’ equilibria in a Gibbs triangle). These features
223 make them useful for projecting relationships between life history traits (e.g., Mims et al.
224 2010). We created ternary plots for our proxies for body size, adult mortality, and juvenile
225 mortality. Allocation to each of these trait axes for each species was taken as their relative
226 location across the full span of vertebrate life history trait space, with each of these ranges
227 standardized to a new axis on a 0-100 scale. We then discretized this space into 16 equal
228 triangles (4 bins for each trait) representing the possible states that each species in our
229 dataset could occupy. This defined life-history space enables us to employ a discrete-state
230 evolutionary model. By doubling the state space and allowing transitions between “layers”
231 defined by binary characters, we can compare how such binary factors influence life history
232 evolution across vertebrates. For example, we defined a 32-state continuous-time Markov
233 chain with two ternary plot spaces corresponding to aquatic and terrestrial life history
234 (Figure 1).

235 We then estimated transitions between aquatic and terrestrial environments, and between
236 regions of the life history space assuming that movement within this space is only allowed
237 between discrete bins that neighbor each other with a shared edge. Transitions in the binary
238 character move species to corresponding bins in the replicated ternary space for the
239 alternative binary state (Figure 1). Since a 32 by 32 transition matrix would have an
240 exceptionally large number of parameters under most models, we simplified movement
241 within each ternary space by defining four parameters governing the dynamics of trait
242 change. These parameters are defined by the directional trends toward each of the three
243 vertices of the space, as well as an overall parameter governing whether species are

attracted or repelled to the center of the triangle (see Supplement). Each layer of the life history space is defined by four unique parameters plus two parameters for asymmetric transitions in the binary trait, for a total of 10 parameters.

We conducted a second set of analyses that accommodate missing data in our three life history proxies by coding their location within the state space with ambiguous coding, which can be modeled using continuous-time Markov Chains. When modeled in this way, the posterior probabilities of species with missing data are computed jointly and is informed by both their observed life history values, as well as the life history values of related species (see supplementary material). All analyses were performed in R using the *fit_mk* function in the castor package modified to account for ternary space (R Core Team 2023).

RESULTS

We identified a three-way trade-off on the bounds of the relationship between offspring mortality, adult mortality, and body size (Figure S1), suggesting an alternative phylogenetic framework for studying constraints on life history evolution in vertebrates. Assuming that over the course of vertebrate evolution, the bounds on vertebrate life history extremes have largely been reached by the species in our dataset, we reformulated the bounded state space of life history as a “Ternary plot” – equilateral triangles that define a space based on trade-offs in investment among these interacting variables (Grime 1974). Placing each species in subdivided locations of this common space then allowed us to explore transitions among locations and quantify which direction of transitions are more common over evolutionary time. With this approach, we address whether the evolutionary significance of transitions from oviparity to viviparity differ among aquatic and terrestrial environments.

Life-history patterns in aquatic and terrestrial environments:-We used phylogenetic comparative tests to identify constraints on the value of traits in life-history space. By focusing on defining these constraints and the "arena" for life history evolution, as opposed to variation in the rates of change, we uncovered fundamental shifts in life history across vertebrates due to transitions between aquatic and terrestrial life histories. Larger vertebrates have lower mortality, as expected, but for aquatic and terrestrial organisms this is achieved through different means (Figure 2). Terrestrial vertebrates have low juvenile mortality regardless of body size but exhibit a steep negative relationship between body size and adult mortality ($\beta = -0.04$, $\beta = -0.58$ respectively, $p < 0.001$, Figure 2A, 2B). In contrast, species with aquatic offspring show a large reduction in juvenile mortality with increasing body size, and low adult mortality across taxa with a weak negative relationship with body size ($\beta = -0.40$, $\beta = -0.17$ respectively, $p < 0.001$, Figure 2A, 2B). When taken together however, aquatic and terrestrial species exhibit highly concordant patterns of lifetime mortality with body size ($\beta = -0.54, \beta = -0.57$ respectively, $p = 0.29$, Figure 2C). Body size and environment explain over a half of the variation ($R^2_{adj} = 0.57$) in juvenile mortality of vertebrates, and over a third of the variation in adult ($R^2_{adj} = 0.41$) and lifetime mortality ($R^2_{adj} = 0.37$).

These analyses additionally highlighted key trade-offs among life history traits depend on the scale of comparisons (Simpson 1951, Reznick et al. 2000, Uyeda et al. 2018). For example, while non-phylogenetic estimates of the covariance between body size, adult mortality, and juvenile mortality are all strongly negative, phylogenetic estimates vary between negative and positive for most traits (except size and adult mortality, which were negatively related in both types of analyses). We found size and both juvenile mortality or

289 adult mortality have a positive evolutionary correlation, but strong negative correlations in
290 the non-phylogenetic analyses. This disparity in the direction of trade-offs suggests a
291 contrast between the evolutionary dynamics between closely related species and the
292 overall bounds on the relationship, which is likewise apparent by visual inspection of the
293 relationships between variables (Figure 2, S4). This difference emerges because while
294 evolutionary changes may appear positively or negatively correlated in the short term, the
295 full space of life history variables in vertebrates is bounded by the fundamental trade-offs
296 that become visible in the non-phylogenetic regressions (and overall examining of the life
297 history space ordinated across species).

298 ***Parity mode evolution in aquatic and terrestrial environments:-***When modelling life-history
299 evolution in ternary space, we found fundamental differences in the evolutionary
300 consequences of transitions to viviparity in each environment. Overall, aquatic species can
301 occupy virtually any space in life-history space, whereas terrestrial species have strong
302 selection pressure to evolve toward reduced adult and juvenile mortality and larger body
303 size (Figure 3). In both environments, while oviparity does not appear to exert strong
304 constraints on life-history strategies, transitions to viviparity are associated with reduced
305 adult and juvenile mortality and larger body size (Figure 4). This shift is explained by
306 movement to a common location within the life-history triangle, despite different starting
307 points within oviparous ancestors. However, for aquatic species, transitions from oviparity
308 to viviparity are typically accompanied by reductions in adult and juvenile mortality, and
309 larger body sizes (Figure 5, 7). By contrast, for terrestrial species, viviparity is associated with
310 a much smaller shift in life-history space (Figure 6, 7). In sum, we infer that while aquatic

environments permit the evolution of more diverse life histories, the evolution of viviparity constrains life history traits more for aquatic species than terrestrial environments.

DISCUSSION

Here we present a novel framework for studying life history evolution that quantifies how developmental and reproductive strategies of aquatic and terrestrial vertebrates have been shaped by contrasting fitness landscapes throughout their radiation. Specifically, transitions from egg laying to live birth represents a major shift across life-history space for aquatic organisms, whereas terrestrial egg-laying organisms are situated adjacent to viviparous strategists and evolve live birth in response to environmental pressures more as a means to remain in that region of life-history space. Our analysis is based on a unique trait-based approach to classifying species based on three metrics, or components of fitness, which can inform comparative studies that seek to explain life history evolution across a broad range of taxa. Ultimately, our three metrics simplify life history space over macroevolutionary time and highlight the long-term constraints on vertebrate diversity.

Overall, the selection pressures that favour live birth, as well as the benefits conferred, are different in the water versus on land. In aquatic environments the evolution of viviparity necessitates the precursory evolution of internal fertilization (Gross and Shine 1981, Beck 1998, Kalinka 2015, Benun Sutton and Wilson 2019). The origins and advantages of internal fertilization are unclear; female choice, male opportunity to manipulate female investment, sperm storage, increased control over fertilization timing, and reduced egg mortality have all been suggested as potential benefits (Orr and Brennan 2015, Lyons et al. 2021). Viviparity in aquatic species acts to increase juvenile survival. Terrestrial organisms, in contrast, have already evolved the necessary preadaptation for live birth; internal fertilization is a

prerequisite of life on land. Moreover, terrestrial vertebrates have already evolved life-history strategies that effectively minimize juvenile mortality. Terrestrial egg deposition requires larger eggs to prevent desiccation, which prolongs developmental times, which in turn favours extended parental care. Animals on land are not bathed in a nutrient broth as they are in aquatic systems, thus precluding particularly small offspring. As such, viviparity on land does not appreciably reduce juvenile mortality, but instead acts more to maintain high levels of juvenile survival across a wider range of environmental conditions.

Differences in life-history diversity and evolution in water versus on land carry important implications for the adaptive capacity of species to environmental change (Forster et al. 2012, Kuparinen and Festa-Bianchet 2017). Firstly, terrestrial environments permit a greatly reduced diversity of life-history strategies. As a result, terrestrial vertebrates will be more vulnerable to global change. Secondly, when considering the relative difference in vulnerability between egg-laying and live-bearing taxa, environmental considerations are paramount. Terrestrial live bearers have similar life-history traits to their egg-laying counterparts, and thus will show comparable response to anthropogenic threats, all else being equal. In contrast, the large shift in life-history strategies seen as viviparity evolves from oviparity in aquatic species suggests their response to threats may be starkly different. For cartilaginous fish, the evolution of live birth represents a distinct shift to a ‘slower’ life history strategy, reducing their adaptive capacity to rapid environmental change (though this may be mediated by an increased capacity for dispersal). For bony fish, however, live birth appears to have evolved to keep pace with highly stochastic, ephemeral environments. As such, their adaptive capacity in the face of anthropogenic threats may be greater than oviparous species.

357 Strong linear relationships (Figure 2) and a triangular distribution of strategies (Figure S1)
358 indicate that long term macroevolutionary patterns are highly directional and that three
359 axes are sufficient to define the vertebrate trait space. Phylogenetically corrected analyses
360 showed less clearly defined trade-offs between the three axes (Figure S4), suggesting that
361 evolution over the short term is not constrained by classic life-history trade-offs between
362 growth, survival, and reproduction (Reznick et al. 2000, Chang et al. 2023). The ubiquitous
363 positive relationship between body size and clutch size within clades serves to highlight this
364 notion (Shine 1988a). Individual clades may have different constraints, but they are all
365 limited to a common space. Indeed, by defining the common life-history space of all
366 vertebrates we provide a useful way to summarize the limits of evolution within a clade.
367 Although the overarching constraint is the inability for species to evolve into 'Darwinian
368 demons' which do not face trade-offs between growth, reproduction, and survival, here we
369 show that life-history space is filled by different clades in different ways and at different
370 rates. Only by understanding the macroevolutionary trade-offs that define trait space does
371 the challenge of comparing such a diaspora of organisms become tractable; disparities in
372 how species move through space can be used to answer questions about which traits are
373 key levers controlling diversification.

374 Fundamentally, placing species in a common life-history framework helps us to understand
375 the rules of life. Once all species are mapped in trait space, one can model
376 macroevolutionary dynamics and explore covariance between key life-history traits. For
377 example, we show that the evolution of viviparity in aquatic and terrestrial environments
378 precedes through different paths and at different rates. Our framework could also be used
379 to understand how differences in food web structure in aquatic and terrestrial

environments shapes life-history strategies. Productivity, the patchiness of resources, and the distribution of predators will have profound implications for both a species' movement through life-history space and the position of life-history optima. Lastly, a potentially fruitful application of this work are species invasions – in our framework, it will be possible to predict shifts in trait-space following the introduction of a non-native species. If species are typically on the edge of replacement, they will likely not be able invest in one of the trait axes (larger body size, higher survival, increased reproductive output) without some kind of ecological release that temporarily relaxes constraints in trait space. For example, the colonization of land, and the ability of viviparous species to exploit cold climates exemplify the interplay between life-history evolution and ecological opportunity. Further research unifying classic life history theory with trait-based approaches and contemporary computational techniques can be leveraged to make progress on previously intractable questions and generate novel insights on the forces that speed up or slow evolutionary innovation.

Data and code availability statement

The dataset and code generated during the current study are available in the Github repository, https://github.com/geobro1992/VTparity

Acknowledgements

We would like to thank Jacob Berman and Ty Stevenson for help compiling trait data. We would like to thank the Department of Fish and Wildlife Conservation and the Department of Biological Sciences at Virginia Tech for financial and logistical support.

402 **Author contributions**

403 GB and HK conceived the idea. GB, HC, and CM compiled and proofed the data. JU designed
404 the analyses. GB, JU, and NB performed the analyses and confirmed the reproducibility of
405 the code and results. GB and HK wrote the manuscript. All authors revised and approved the
406 final manuscript.

407 **Competing Interests Statement**

408 The authors declare no competing interests.

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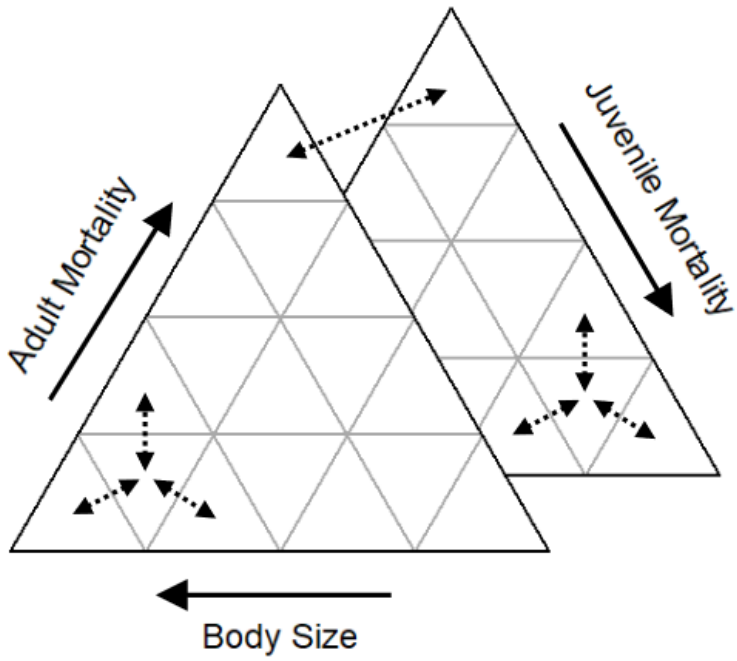
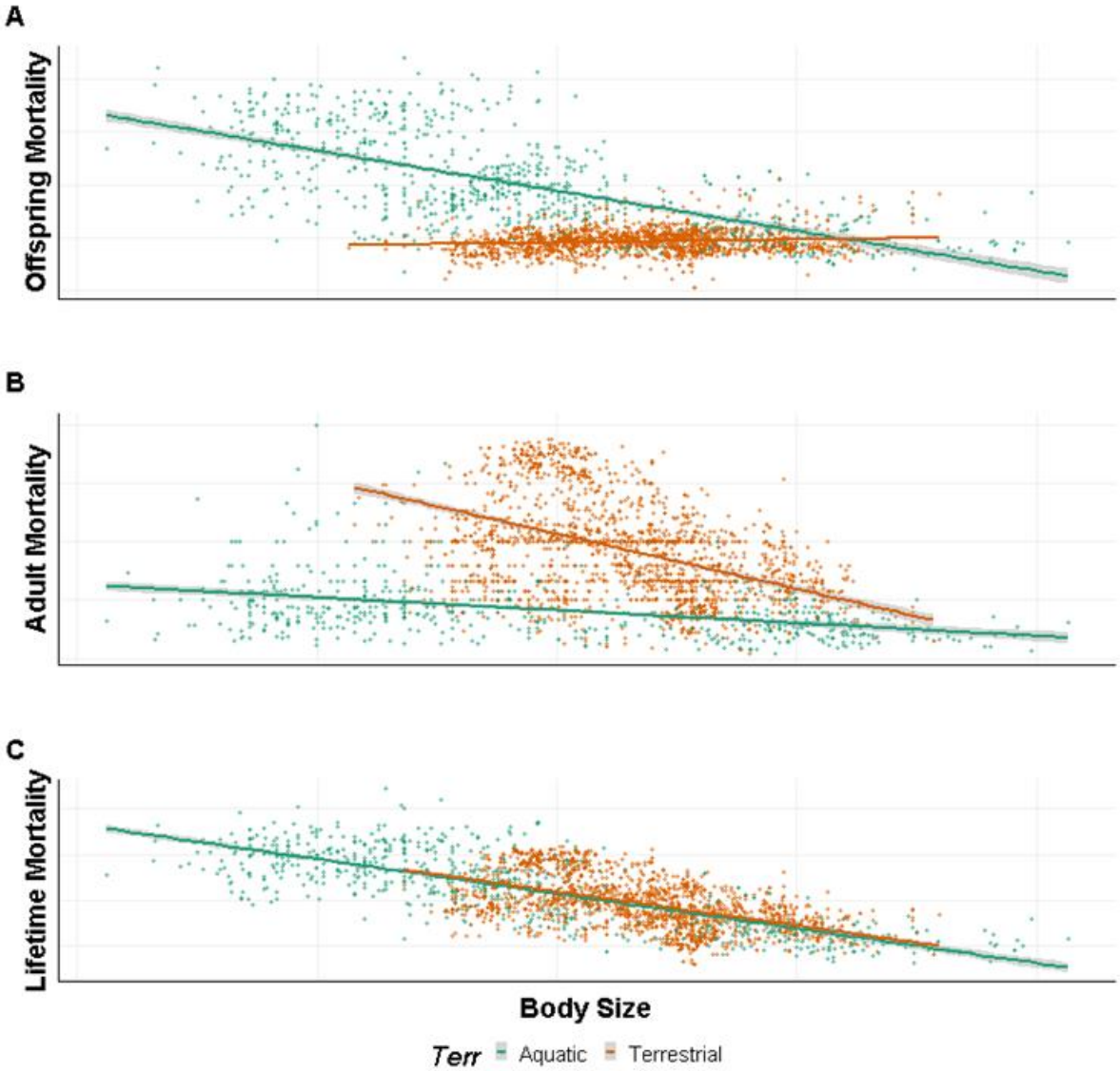


Figure 1. A conceptual diagram of the discrete-space evolutionary model in ternary space. In this modelling framework, species can evolve to neighbouring patches within the defined life-history space or can transition between states. The two state spaces (triangles) can represent egg-laying and live-bearing reproductive modes or aquatic and terrestrial environments.



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553 **Figure 2: The relationship between body size and a) juvenile mortality, b) adult mortality,**

554 **and c) lifetime mortality for aquatic and terrestrial vertebrates. Offspring mortality in**

555 **terrestrial environments is hyper-constrained, and variation in life-histories is chiefly**

556 **explained by changes in adult mortality. Regression lines account for phylogenetic**

557 **relatedness.**

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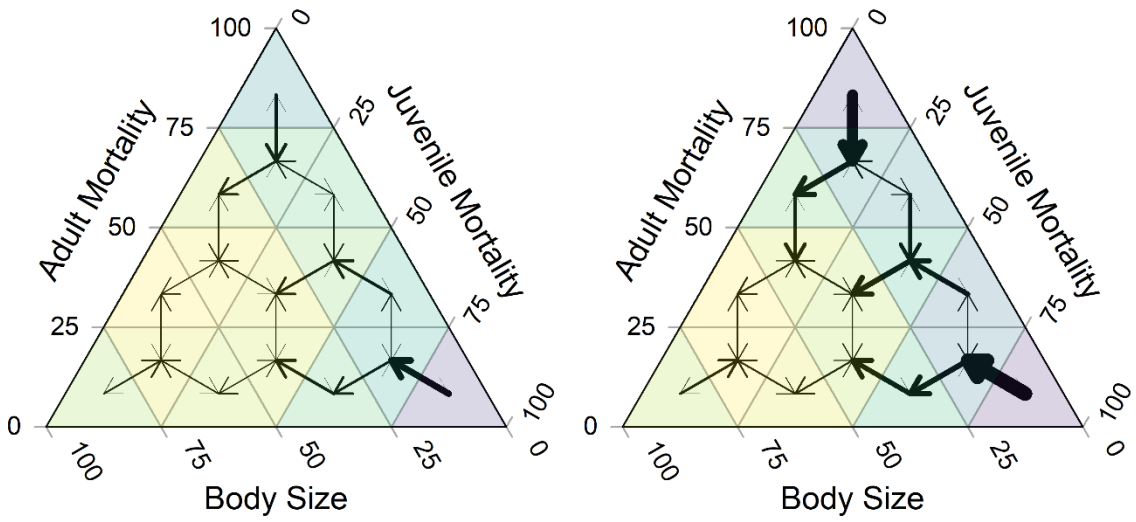


Figure 3: Movement through life-history space for aquatic (left) and terrestrial (right) vertebrates. Plots were generated from 2922 species for which life-history data was available. The colours represent the number of taxa represented in each segment, with darker colours representing fewer species, and lighter colours representing more species. The arrows indicate the direction and relative strength of selection through life-history space.

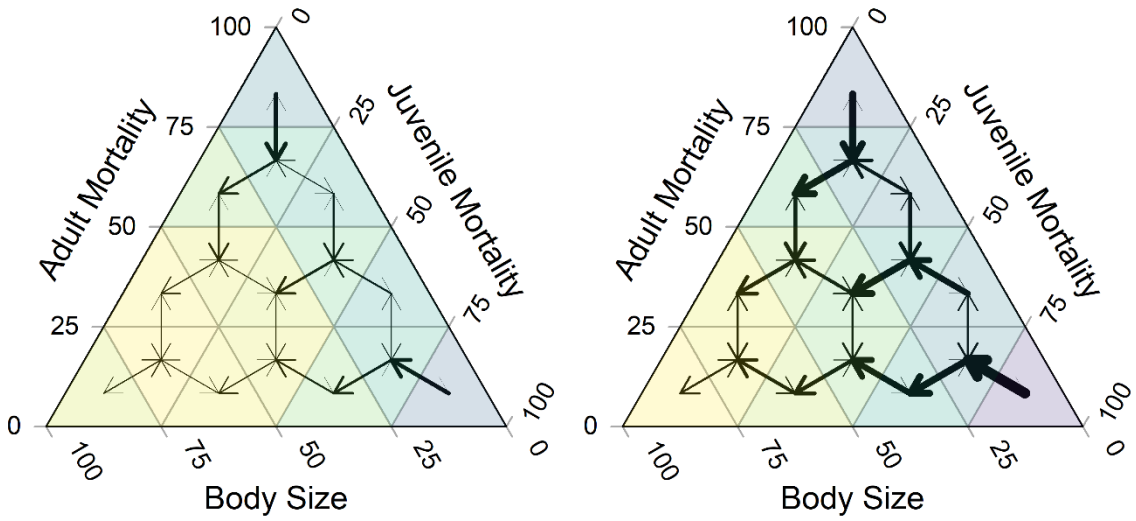
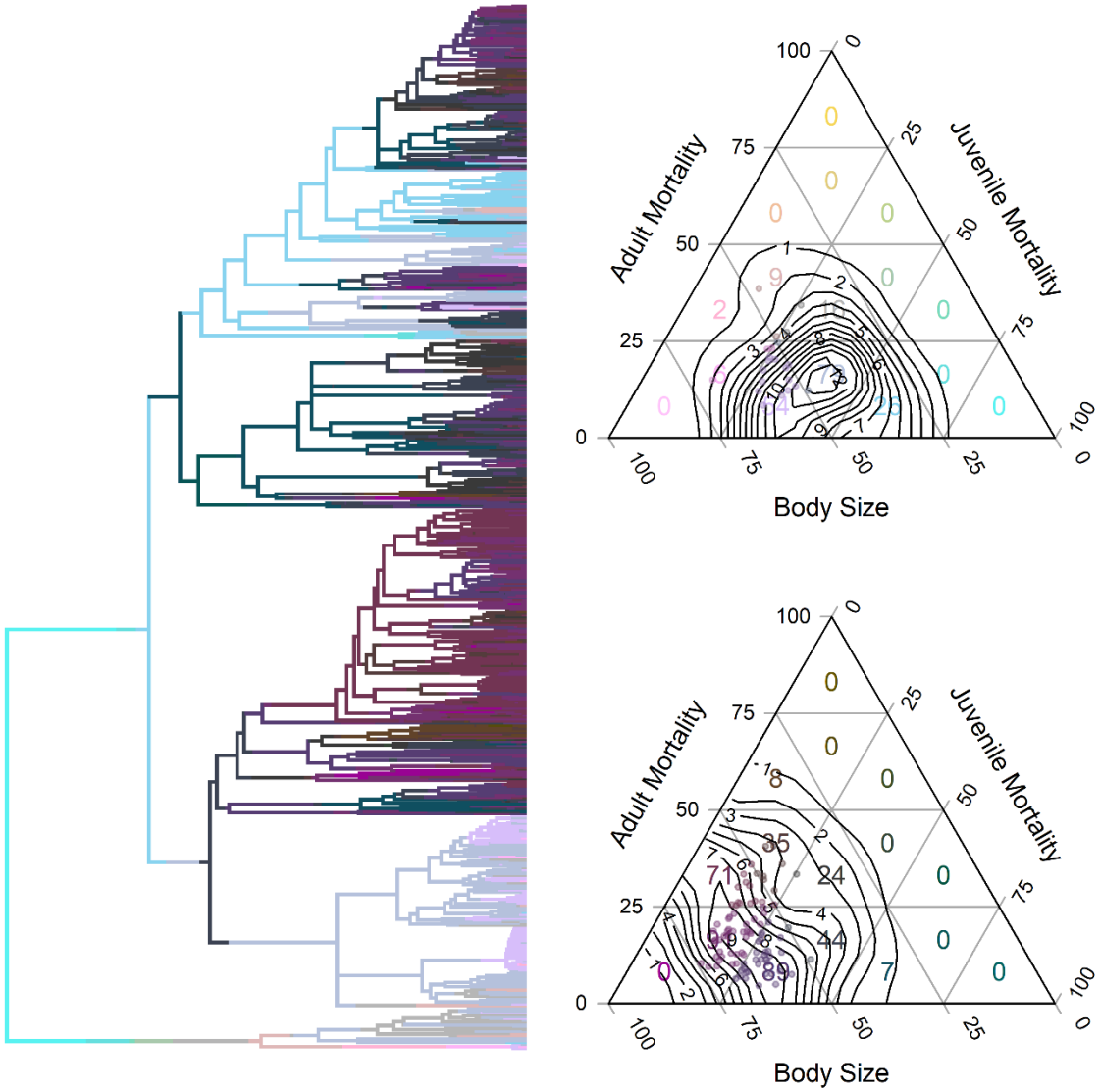


Figure 4: Movement through life-history space for egg-laying (left) and live-bearing (right) vertebrates. Plots were generated from 2922 species for which life-history data was available. The colours represent the number of taxa represented in each segment, with darker colours representing fewer species, and lighter colours representing more species. The arrows indicate the direction and relative strength of selection through life-history space.



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577 **Figure 5. Phylogeny (left) of cartilaginous fishes (sharks, rays, and chimaeras) and the**

578 **relative position in life-history space for egg-laying (top right) and live-bearing (bottom**

579 **right) taxa. Ternary plots show the counts of species in each segment with overlaid**

580 **contours indicating the density of species in life-history space. The branches of the**

581 **phylogeny are coloured to match the ternary plots.**

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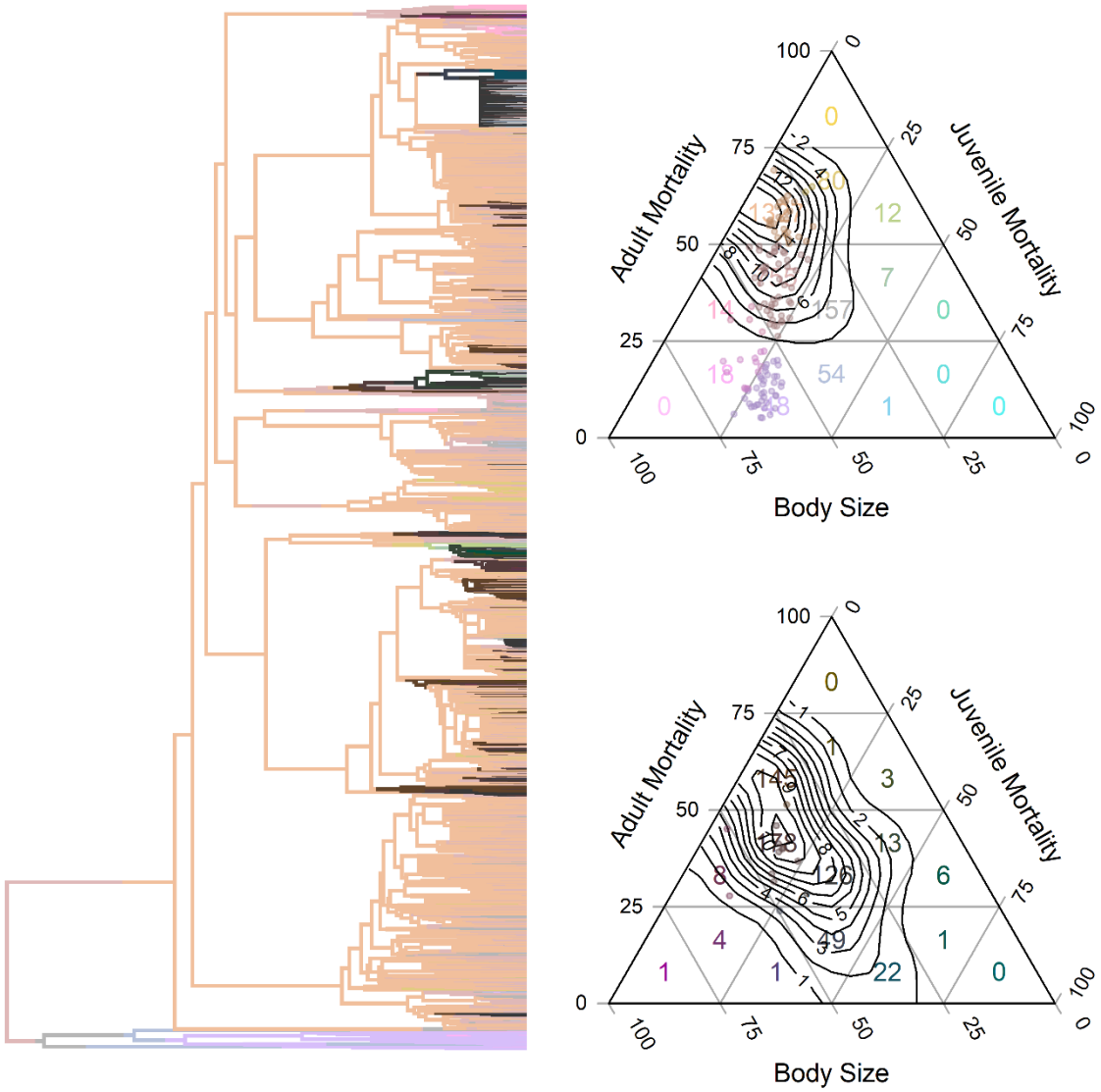

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584 **Figure 6. Phylogeny (left) of reptiles and the relative position in life-history space for egg-**

585 **laying (top right) and live-bearing (bottom right) taxa. Ternary plots show the counts of**

586 **species in each segment with overlaid contours indicating the density of species in life-**

587 **history space. The branches of the phylogeny are coloured to match the ternary plots.**

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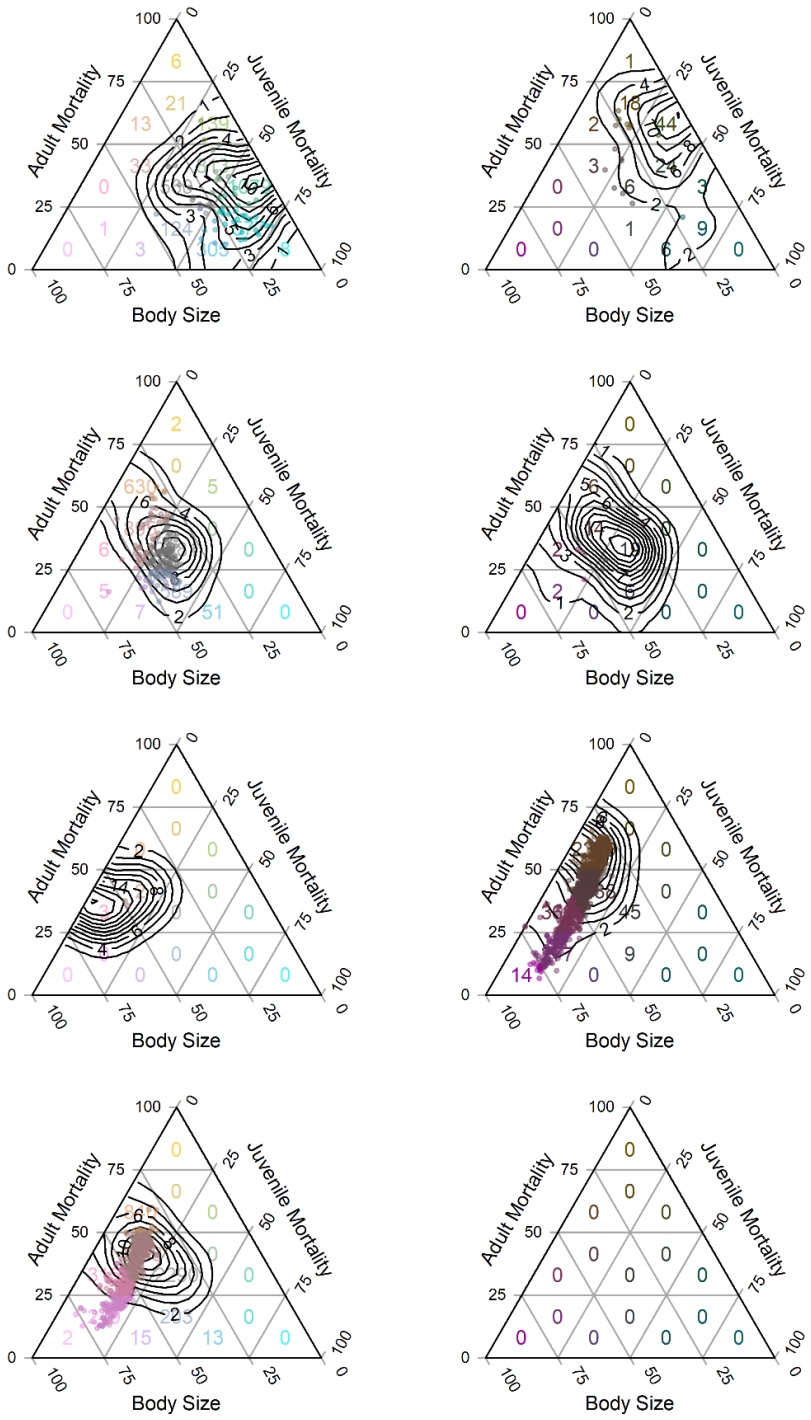

Figure 7. Comparison of egg-laying (left) and live-bearing (right) species of bony fish (top row), amphibians (second row), mammals (third row), and birds (bottom row). Ternary plots show the counts of species in each segment with overlaid contours indicating the density of species in life-history space.