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RESEARCH ARTICLE

Evolution of reproductive modes in sharks and rays

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Abstract

The ecological and life history drivers of the diversification of reproductive modes in early vertebrates are not fully understood. Sharks, rays and chimaeras (group Chondrichthyes) have an unusually diverse variety of reproductive modes and are thus an ideal group to test the factors driving the evolution of reproductive complexity. Here, using 960 species representing all major Chondrichthyes taxa, we reconstruct the evolution of their reproduction modes and investigate the ecological and life history predictors of reproduction. We show that the ancestral Chondrichthyes state was egg-laying and find multiple independent transitions between egg-laying and live-bearing via an intermediate state of yolk-only live-bearing. Using phylogenetically informed analysis, we also show that live-bearing species have larger body size and larger offspring than egg-laying species. In addition, live-bearing species are distributed over shallow to intermediate depths, while egg-layers are typically found in deeper waters. This suggests that live-bearing is more closely associated with pelagic, rather than demersal habitats. Taken together, using a basal vertebrate group as a model, we demonstrate how reproductive mode co-evolves with environmental conditions and life-history traits.

KEYWORDS

life history evolution, phylogenetic comparative methods, reproductive modes, sharks and rays

1 | INTRODUCTION

Vertebrates exhibit an impressive diversity of reproductive modes, including variation in modes of parturition and nutrient provision to the developing offspring (Blackburn, 1999; Kupfer et al., 2016; Pyron & Burbrink 2013; Vági et al., 2019). In egg-laying (oviparous)

species, the embryos develop mostly externally. This form of reproduction is common in chondrichthyes, teleosts, amphibians, reptiles, and birds. The offspring of live-bearing (viviparous) species develop inside the mother until birth (Shine, 1995); this form of reproduction is dominant in mammals, but also occurs in some amphibians, squamates, bony fishes and sharks. In all oviparous and

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many viviparous species, the only maternal source of nutrition provided to the embryo is the yolk-sac. However, many other viviparous lineages have evolved alternative pathways of nutrition for the developing embryos, such as placental viviparity in mammals, and in sharks and rays (see below). Although transitions to live-bearing are considered a key innovation that led to a burst of diversification in several vertebrate lineages (Helmstetter et al., 2016; Mank & Avise, 2006; Organ et al., 2009; Pyron & Burbrink, 2013), the factors influencing these transitions are not yet fully understood. Groups with diverse reproductive strategies are ideal for studying this question because of the larger number of transitions they underwent, thus allowing for greater statistical power in matching ecological conditions to evolutionary changes (Blackburn, 2006; Buddle et al., 2019; Van Dyke et al., 2014).

In most vertebrate lineages, egg-laying is considered as the ancestral mode of reproduction (Blackburn, 1999; Kupfer et al., 2016; Mank & Avise, 2006; Pyron & Burbrink 2013). Eggs provide some protection for the developing embryo; however, they are vulnerable to predation, dehydration and/or extreme temperatures. Retaining the eggs and carrying them in the oviduct (yolk-only viviparity) provides extra protection from predators and unpredictable or even adverse environmental conditions like suboptimal temperatures (Shine, 1995; Tinkle & Gibbons, 1977). Therefore, the evolution of viviparity is often associated with harsh environments, such as high-latitude, high-altitude or extremely dry habitats (Lodé, 2012; Ma et al., 2018; Shine, 2007). Mothers also benefit from live-bearing by avoiding the costly migration to environments that provide conditions necessary for the developing eggs (Motani, 2005; Neill, 1964). On the other hand, viviparity also has a number of costs. First, it can slow down the reproductive cycle, as the mother cannot produce a new clutch until the current one is born (Shine, 1985a, 1985b; Stearns, 1989; Zera & Harshman, 2001). Second, the limited space inside the mother results in a smaller number of offspring compared to oviparous species (Recknagel & Elmer, 2019). Finally, physically carrying the eggs or offspring inside her body can reduce the mobility of the mother, which is acutely disadvantageous when searching for resources or escaping from predators (Banet et al., 2016; Ghalambor et al., 2004).

Beyond the basic yolk-only viviparity, the evolution of additional offspring nourishment in viviparity is hypothesised to be associated with food availability (Trexler & DeAngelis, 2003; Van Dyke et al., 2014); nonetheless, the drivers of its diversification are still contentious. At least three mechanisms of additional embryonic nourishment are known in vertebrates: oophagy, where the embryo is supplied with additional eggs or embryos (Dopazo & Korenblum, 2000); histotrophy, where maternal secretions or hypertrophic maternal tissues provide food source (Goycochea et al., 1986; Guex & Chen, 1986; Kupfer et al., 2006), and placental viviparity, where nutrients are provided directly from the maternal bloodstream (Wooding & Burton, 2008; Wourms, 1981). In vertebrates, all of these alternatives have evolved several times (Blackburn, 1999; Pollux et al., 2009; Pyron & Burbrink 2013). Nonetheless, the

evolution of diverse reproductive modes is not yet fully understood. Comparative studies in groups where this full diversity is present is a promising avenue to further elucidate this question.

One such group is that of sharks, rays and chimaeras (hereafter, Chondrichthyes). This is one of the oldest radiations of vertebrates, originating from the early Silurian period, approximately 420 million years ago (Benton et al., 2009). It contains 1192 extant species (Stein et al., 2018), which are diverse in body shape, ecology and habitat (Hamlett, 2005). Chondrichthyes species also exhibit a striking diversity of reproductive modes, including (i) egg-laying, (ii) yolk-only viviparity without maternal input, (iii) oophagy, (iv) histotrophy by uterine milk and (v) placental viviparity (Buddle et al., 2021; Castro et al., 2016; Musick & Ellis, 2005; Tomita et al., 2019). By contrast, in most vertebrate clades, the diversity of reproductive modes has been lost predominantly to either oviparity (e.g., in bony fish, amphibians, reptiles and birds), or to placental viviparity (in mammals). This makes the Chondrichthyes an ideal group to investigate the evolution of reproductive modes. Previous studies on this question yielded conflicting results about the number and direction of transitions, as well as the ancestral reproductive mode in the group, which was inferred as either egg-laying or yolk-only live-bearing (Dulvy & Reynolds, 1997; Lund, 1980; Musick & Ellis, 2005). Furthermore, the association between reproductive modes and life-history has never been comprehensively explored in this group. Recent advances, such as new comprehensive phylogenies (Stein et al., 2018) and new statistical methods, now offer a unique opportunity to revisit these questions.

Here, we present the most comprehensive analysis to date of the evolutionary transitions of reproductive modes in sharks and rays. We have three key objectives. First, we aim to reconstruct the ancestral state of the Chondrichthyes group by asking whether the advanced reproductive modes of live-bearing with maternal input evolved from egg-laying or from yolk-only viviparity (Blackburn, 1995; Dulvy & Reynolds, 1997; Lund, 1980; Musick & Ellis, 2005). We expect that, as placental viviparity requires complex anatomical adaptations, it most likely evolved from the intermediate state of yolk-only viviparity. Second, we aim to investigate whether reproductive modes are associated with life history. We hypothesize that viviparous species with maternal input have fewer and larger offspring than species with egg-laying and yolk-only viviparity (Pollux et al., 2009; Thibault & Schultz, 1978). Third, we also test the associations between reproductive modes and the environment. We predict that oviparous species are more likely to live in deeper waters and be bottom-dwellers because oviparous sharks and rays have benthic eggs and are thus tied to seafloor oviposition sites. By contrast, viviparous species can live closer to the surface and in open water habitats throughout their life cycles (Rigby & Sempendorfer, 2013; Wourms, 1993). We also investigated the ancestral Chondrichthyes habitat, predicting that the oviparous ancestors lived on the seafloor, and viviparous species were more capable of colonizing pelagic habitats (Compagno, 1990; Mull et al., 2019; Sorenson et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Data collection

We collected data on reproductive modes from peer-reviewed journals and the Fishbase online database (Froese & Pauly, 2021, see Table S1). We classified the reproductive modes into five distinct categories. The assignment of egg-laying and placental viviparity was straightforward in all cases. If the mother secretes either 'lipid' or 'limited' uterine milk (Hamlett, 2005), we classified both of these categories as live-bearing with uterine milk. We classified species where the mother provides unfertilized eggs to the embryos to feed on as live-bearing with oophagy. Because adelphophagy (sibling cannibalism in the uterus) is considered to be a specific type of oophagy in the literature (Musick & Ellis, 2005) we merged this category with live-bearing with oophagy. When the embryos develop inside the mother and feed solely on yolk (also referred to as ovoviviparity), we classified these as yolk-only live-bearing. In some cases, the difference between uterine milk viviparity and yolk-only viviparity is hard to identify, especially in the dogfish sharks (group Squalomorphii) where yolk-only viviparity is the most widespread mode of reproduction. In some of these species, females may provide limited amounts of mucus to the embryos, but they develop mostly using the yolk (Hamlett, 2005; Musick & Ellis, 2005). Therefore, we classified them as yolk-only live-bearing.

For species with data on reproductive mode, we extracted life-history and environmental data from reference books (e.g. Hamlett, 2005), peer-reviewed journals and Fishbase (Froese & Pauly, 2021). Data on mean adult body size were collected from Pimiento et al. (2019). We collected mean values from the literature for size and number of the offspring (see Data S1). If minima and maxima were given for these quantities, we used their mean. We defined lifespan as the maximum lifespan of the species observed in the wild. In addition, to validate our life history data from Fishbase, for a subset of species we also collected data from the recently published Sharkipedia (<https://www.sharkipedia.org/>, Mull et al., 2022), and we investigated the consistency of the two sources.

We also extracted two types of environmental data from Fishbase (Froese & Pauly, 2021): (i) using the minimum and maximum water depth, we calculated the mean depth of each species and (ii) ascertained their habitat type (see Table S2).

2.2 | Statistical analyses

We used a sample of 100 phylogenetic trees, downloaded from VertLife.org (<https://vertlife.org/>, Stein et al., 2018), a molecular-based phylogeny database containing 1193 recognized species of sharks and rays. We mapped the ancestral states of both reproductive mode and habitat using the 'make.simmap' function in the 'phytools' package in R (R Core Team 2014; Revell, 2012). In 'make.simmap', we used three different models using the 100 phylogenetic

trees: the equal rates model (ER), where only equal transition rates are allowed between the character states; the symmetric model (SYM), where equal transition rates are allowed between the character states but rates can vary across different character pairs; and the all rates different model (ARD), where different transition rates are allowed between the states. The relative fit for each model was compared using the Akaike information criterion (AIC; Akaike 1973). We calculated the number of evolutionary transitions between reproductive modes of the ancestral state reproduction model with the lowest AIC using the 'make.simmap' function. We counted the mean number of evolutionary transitions out of the 100 repeats, then we calculated the relative frequency of transitions as the number of transitions divided by the mean number of occurrences of the initial state.

In order to investigate the overall effect of reproductive mode on the response variables we carried out phylogenetic ANOVA. To investigate the associations of reproductive mode with life history and ecological variables, we fitted phylogenetic generalized least squares (PGLS) models using the package "caper" (Orme & Freckleton, 2013). Bivariate models were used because the predictor variables showed a high level of correlation (pairwise correlation test, Table S3). We tested six bivariate models in which reproductive mode was a categorical predictor (either egg-laying, yolk-only live-bearing or live-bearing with maternal input, with egg-laying as the reference category), and the following response variables: (i) body length; (ii) life span; (iii) offspring size; (iv) offspring number; (v) water depth; and (vi) habitat type (see Table 1). We used reproductive mode as the predictor in the models because in PGLS the response variable must be a continuous variable. In all models, numerical life history variables were log-transformed and habitat type was treated as a numeric ordinal variable with possible values of 1 (demersal, i.e. bottom-living species which are generally more associated with a deepwater bottom-living lifestyle but which also includes species living at shallower depths, for instance in coral reefs), 2 (opportunistic, i.e. species that move around, visiting both demersal, and open-water habitats), or 3 (pelagic, i.e. open-water species, which live higher up in the water column). To test the robustness of our results, we also ran these models using two subsets of the data, randomly selected to contain 80% and 60% of the total data for each variable. We ran 100 repeats of each of the above models (see Tables S4 and S5, respectively).

3 | RESULTS

3.1 | Diversity of reproductive modes in sharks and rays

We found data on reproductive modes for 960 of the 1193 known extant species (Figure 1; Table S1; Figures S1 and S2). Two groups in particular show high diversity (Figure S3): approximately half of skates and rays (Batoidea) are egg-laying, while the other half

TABLE 1 Definitions of reproductive modes in sharks, rays and chimaeras.

Reproductive mode	Definition
Egg-laying	Offspring develops in a leathery egg case externally, nourishment is provided by the yolk sac, e.g., <i>Hydrolagus collicii</i> , <i>Heterodontus francisci</i> , <i>Scyliorhinus canicula</i> , <i>Amblyraja hyperborea</i>
Live bearing	
Yolk-only viviparity	Offspring develops inside the mother, nourishment is provided by the yolk sac, e.g., <i>Mobula birostris</i> , <i>Rhincodon typus</i>
Live-bearing with maternal input	
Live-bearing with oophagy	Offspring develops inside the mother, nourishment is provided by the yolk sac, and after the yolk is fully absorbed embryos feed on unfertilised eggs, e.g., <i>Alopias pelagicus</i> , <i>Isurus oxyrinchus</i> , or the embryos cannibalize each other (adelphophagy), e.g., <i>Carcharias taurus</i> , <i>Lamna nasus</i>
Live-bearing with uterine milk	Offspring develops inside the mother, nourishment is provided by the yolk sac and 'uterine milk' secreted by the mother. This 'milk' could be of either 'limited' type, where embryos feed on uterine mucus, or 'lipid' type, where embryos feed on lipid and protein-rich substances, e.g., <i>Carcharodon carcharias</i> , <i>Rhynchobatus australiae</i> , <i>Myliobatis australis</i>
Live-bearing with placenta	Offspring develops inside the mother, nourishment is filtered from the circulatory system of the mother via a placental connection, e.g., <i>Mustelus canis</i> , <i>Carcharhinus amblyrhynchos</i> , <i>Sphyrna mokarran</i>

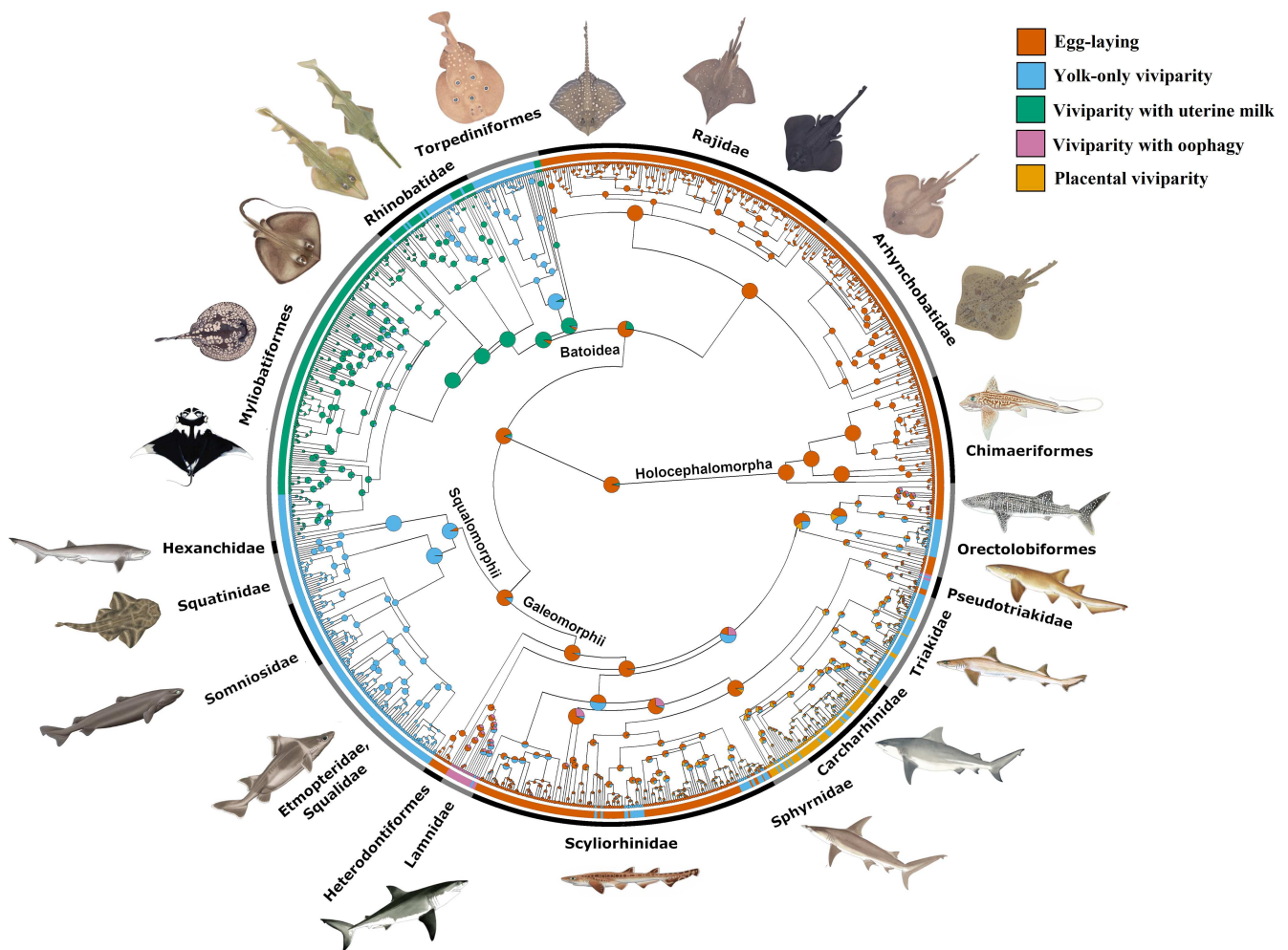


FIGURE 1 Reproductive modes in sharks, rays and chimaeras based on 100 stochastic character mapping simulations using the equal rates model of 'phytools' (Revell, 2012). Pie charts indicate the likelihood of reproductive modes at a given node, and the central node represents the common ancestor of sharks, rays, and chimaeras. Species illustrations are from Last et al. (2016) and Ebert and Dano (2020).

are either yolk-only or uterine milk-producing live-bearing species. In addition, most galeomorph sharks (Galeomorphii) are live-bearing (yolk-only, placental or oophagy), with fewer species being

egg-layers. In contrast, squalomorph sharks (Squalomorphii) and chimaeras (Holocephalomorpha) have invariable reproductive modes with yolk-only live-bearing and egg-laying, respectively.

3.2 | Ancestral state of reproductive modes

We inferred that the ancestral reproductive mode of both sharks and rays, and indeed the entire Chondrichthyes group is egg-laying (Figure 1), consistent with Dulvy and Reynolds (1997). Yolk-only live-bearing and live-bearing with uterine milk originated closer to the basal nodes, whereas oophagy and placental live-bearing emerged later. Live-bearing with maternal input emerged later. Live-bearing with maternal input is inferred to have evolved both from yolk-only live-bearing and directly from egg-laying (Figure 2). Furthermore, live-bearing with maternal input could have reverted to yolk-only live-bearing and the latter could have reverted further back to egg-laying in some species (Figure 2). Importantly, we did not infer any direct reversal from live-bearing with maternal input to egg-laying (Figure 2). Only one direct transition was inferred between different forms of live-bearing with maternal input, when placental live-bearing transitioned to live-bearing with uterine milk in tiger sharks (*Galeocerdo cuvier*, Carcharhinidae). The model with the best fit (lowest AIC) of ancestral state reconstruction was the equal rates model (ER, $AIC_c = 423.19$), followed by the symmetric model (SYM, $AIC_c = 423.42$) and all rates different model (ARD, $AIC_c = 465.37$, Figures S4–S6).

3.3 | Association between reproductive mode, life history and ecology

Body size, life span and offspring size are significantly associated with reproductive mode (Table 2). Specifically, egg-laying sharks and rays have significantly smaller bodies, shorter life spans and smaller offspring than species with yolk-only live-bearing. Live-bearing species with maternal input have shorter life spans than species with yolk-only viviparity, and fewer but larger offspring than egg-laying species (Figure 3, Table 2; note that data on life span were sparser [$N = 99$ species] than other life-history variables). These associations between reproductive modes and body length, life span and offspring size remained consistent when the models were repeated with a random sample of both 80% and 60% of species (Tables S4 and S5), underlining the robustness of the results.

Water depth and life-style show weak or non-significant associations with reproductive mode, respectively (Figure 4). Although live-bearing species tend to live closer to the water surface whereas egg-layers typically live deeper down (Table 2, Figure S7), these associations are no longer significant when re-sampling with 80% or 60% of the data (Tables S4 and S5). The

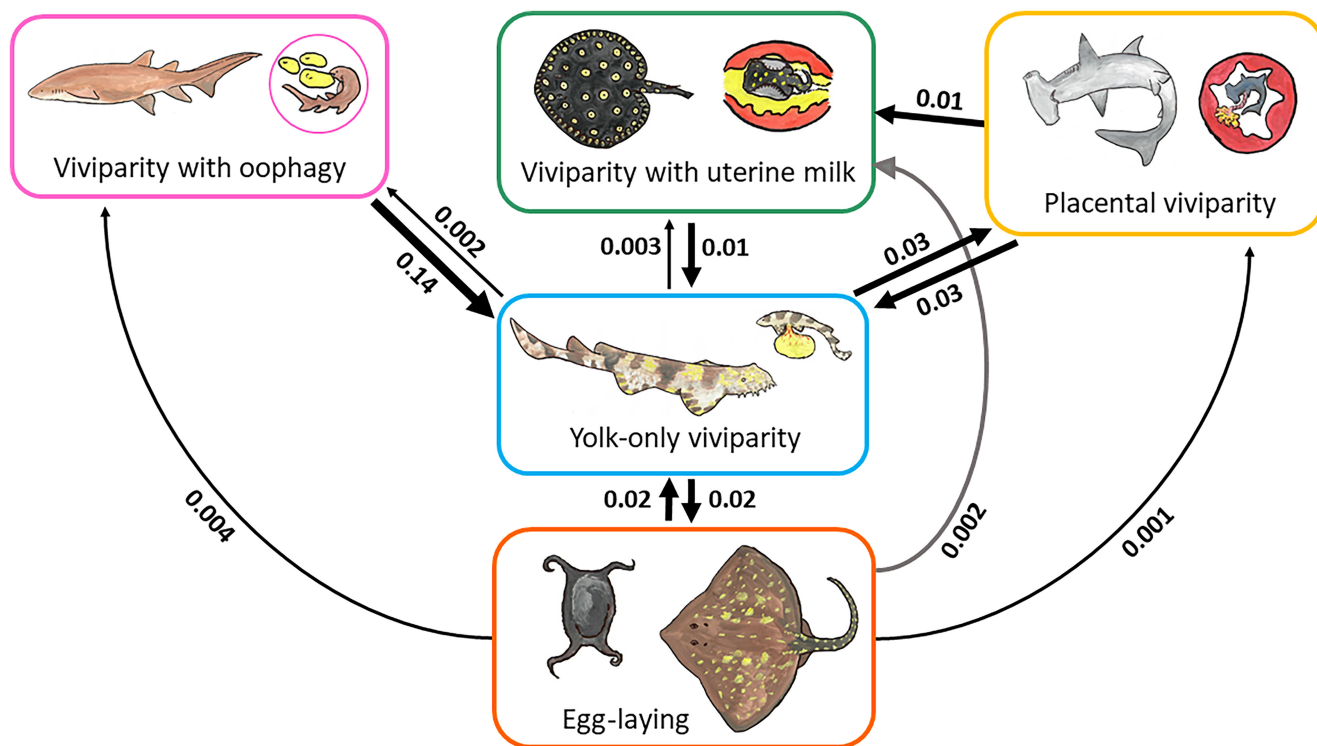


FIGURE 2 Evolutionary transitions between reproductive modes in sharks, rays and chimaeras based on 100 stochastic character mapping simulations using the equal rates model in 'phytools' (Revell, 2012). The numbers represent the calculated rate of transitions between each reproductive mode (the number of transitions divided by the number in each initial reproduction state). Illustrated species: egg laying: thornback ray (*Raja clavata*, Rajidae); yolk-only viviparity: ornate wobbegong (*Orectolobus ornatus*, Orectolobidae); viviparity with oophagy: tawny nurse shark (*Nebrius ferrugineus*, Ginglymostomatidae); viviparity with uterine milk: Xingu River ray (*Potamotrygon leopoldi*, Potamotrygonidae); placental viviparity: smooth hammerhead (*Sphyrna zygaena*, Sphyrnidae).

TABLE 2 Relationships between life history traits, environment and reproductive modes in Chondrichthyes.

Response variable	<i>F</i>	<i>p</i>	λ	Comparisons between reproductive modes	$\beta \pm SE$	<i>p</i>
Body length (<i>N</i> =397)	3.5	0.03	0.85	Egg-laying versus yolk-only viviparity	0.54 ± 0.20	0.008
				Egg-laying versus maternal input viviparity	0.32 ± 0.23	0.16
				Yolk-only viviparity versus maternal input viviparity	-0.21 ± 0.16	0.17
Life span (<i>N</i> =99)	3.01	0.05	0.0	Egg-laying versus yolk-only viviparity	0.53 ± 0.17	0.002
				Egg-laying versus maternal input viviparity	0.24 ± 0.15	0.12
				Yolk-only viviparity versus maternal input viviparity	-0.29 ± 0.11	0.02
Offspring size (<i>N</i> =241)	5.5	0.004	0.83	Egg-laying versus yolk-only viviparity	0.43 ± 0.16	0.01
				Egg-laying versus maternal input viviparity	0.54 ± 0.18	0.003
				Yolk-only viviparity versus maternal input viviparity	0.11 ± 0.10	0.28
Offspring number (<i>N</i> =279)	1.22	0.29	0.8	Egg-laying versus yolk-only viviparity	0.29 ± 0.26	0.25
				Egg-laying versus maternal input viviparity	-0.07 ± 0.30	0.80
				Yolk-only viviparity versus maternal input viviparity	-0.37 ± 0.18	0.04
Water depth (<i>N</i> =832)	0.64	0.05	0.86	Egg-laying versus yolk-only viviparity	0.58 ± 0.22	0.01
				Egg-laying - maternal input viviparity	0.92 ± 0.27	0.009
				Yolk-only viviparity - maternal input viviparity	-0.07 ± 0.30	0.8
Life style (<i>N</i> =958)	0.02	0.97	0.679	Egg-laying versus yolk-only viviparity	0.01 ± 0.11	0.88
				Egg-laying versus maternal input viviparity	-0.04 ± 0.14	0.97
				Yolk-only viviparity versus maternal input viviparity	-0.02 ± 0.1	0.83

Note: For phylogenetic ANOVA we provide the *F* value (*F*), and corresponding *p*-value. Categories are compared with phylogenetic generalized least squares (PGLS) using egg-laying or yolk-only live-bearing as reference category, and we provide parameter estimates with standard error ($\beta \pm SE$), the corresponding *p*-value, and Pagel's lambda (λ). Life history variables were log₁₀ transformed prior to the analyses. *N* refers to the number of species, and significant associations are in bold.

ancestral species are inferred to live close to the bottom, whereas the colonization of open waters, coasts, and coral reefs occurred later (Figure S8; equal rates model AIC_c=1694.56, symmetric model AIC_c=1999.33, all rates different model AIC_c=2107.52; Figures S9 and S10).

Importantly, data from Sharkipedia and FishBase are highly correlated (Table S6). Thus, our results are robust to the database used.

4 | DISCUSSION

4.1 | Ancestral state and transitions among reproductive modes

To our knowledge, this is as yet the most comprehensive phylogenetic analysis of reproductive modes and their association with life history and environmental variables in a basal vertebrate group.

Our comprehensive phylogenetic analysis revealed three key results. First, our results support the overall finding of Dulvy and Reynolds (1997) that egg-laying was the ancestral reproductive mode in Chondrichthyes, however we found two key differences. We show that egg-laying was the ancestral state of skates (Rajidae), in contrast to Dulvy and Reynolds (1997) who inferred live-bearing as the ancestral state in this group. In addition, our results suggest that in carpet sharks (Orectolobiformes), egg-laying did not revert from live-bearing. Differences between our results and those reported

by Dulvy and Reynolds (1997) may be explained by our more comprehensive taxonomic coverage, higher data resolution due to using species-level data only, more sensitive statistical methods and updated phylogenetic hypotheses.

Second, apart from the exclusively egg-laying group of ghost sharks and chimaeras, yolk-only viviparity evolved in all other major groups, while live-bearing with maternal input evolved in rays and in galeomorph sharks. We found that, in most cases, yolk-only live-bearing was an intermediate state from which all three types of live-bearing with maternal input could have evolved. However, despite the fact that live-bearing requires complex adaptations in anatomy, physiology and behaviour for longer retention of eggs, we did infer direct transitions between egg-laying and live-bearing with maternal input, where the yolk-only stage of live-bearing was apparently "skipped" in the galeomorph sharks. Although the latter result was unexpected, it is not unprecedented. In a study on anurans, Gomez-Mestre et al. (2012) found that the intermediate stages in complex reproductive modes are sometimes not detectable, which probably indicates that these existed for relatively short time intervals on an evolutionary time scale.

We classified mixed reproductive modes based on the dominant component of nutrient provision (Hamlett, 2005; Musick & Ellis, 2005), although these are transitional states between yolk-only live-bearing and some form of matrotrophy. Our results showed that the different forms of matrotrophy (uterine milk, oophagy

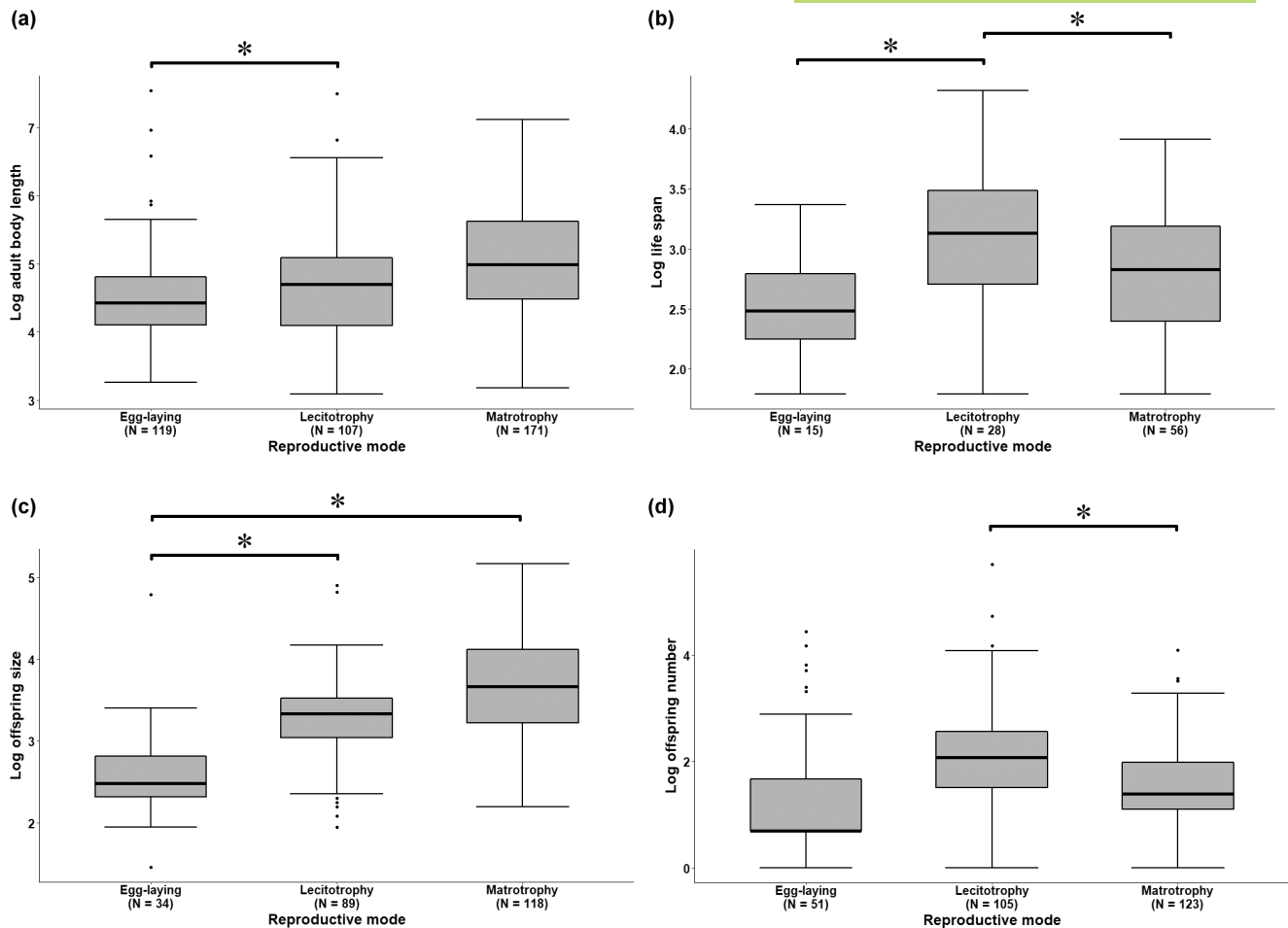


FIGURE 3 Reproductive mode versus life history traits in sharks, rays and chimaeras. (a) Adult body length (\log_{10} m); (b) life span (\log_{10} years); (c) offspring size (\log_{10} cm); (d) number of offspring (\log_{10}). Egg-laying refers to egg-laying species, lecitotrophy refers to yolk only viviparity, and matrotrophy refers to viviparity with maternal input. N refers to the number of species, and asterisk indicates a significant difference. For phylogenetically corrected statistical results, see Table 2. In each box plot, the thick middle line, box and whiskers represent the median, interquartile range and the minimum and maximum data range, respectively, and the circles represent outlier data points.

and placenta) evolved independently, as alternative solutions for offspring provisioning. We identified only one transition between different forms of matrotrophy, when the tiger shark lost its placenta and evolved uterine milk instead (Castro et al., 2016; Swift et al., 2016). Thus, we still do not fully understand the causes of matrotrophy within sharks and rays. As direct transitions between its forms were extremely rare, it is likely that ontogenetic or evolutionary constraints pushed certain chondrichthyan clades towards one form or another.

4.2 | Life history, ecology and reproductive modes

Our third main finding is that live-bearing sharks and rays have larger offspring than egg-laying species, a common pattern across animals (Blackburn, 1999). Offspring can benefit from a large size at birth because they can enter the food web in a higher position. According to our results, matrotrophic species can excel at this. For example, sand-tiger shark (*Carcharias taurus*) offspring are born as powerful

predators with a length of almost one meter, having cannibalized their siblings in utero (Blackburn, 2015). The survival of offspring may also differ between egg-layers and live-bearing species. Large offspring may reach maturity faster and survive better than small offspring that hatched from eggs (Wourms, 1993).

Our findings suggest that ancestral sharks were egg-layers and lived on or close to the seabed, and later species radiated out into open water habitats. As sharks and rays do not produce pelagic buoyant eggs, in contrast to bony fish (Craik & Harwey, 2009; Wourms, 1993), live-bearing may have allowed different lineages of sharks and rays to colonize pelagic environments. Oviparous sharks and rays produce benthic egg cases, and presumably retaining these eggs was less costly than evolving specialized buoyant eggs. Furthermore, carrying the embryos internally might be beneficial in pelagic habitats as the mothers are not tied to oviposition sites (Wourms, 1977; Wourms & Lombardi, 1992). Live-bearing could also be advantageous in environments where there is a high density of individuals, or high diversity of species (e.g., coral reefs or coastal habitats where many live-bearing species

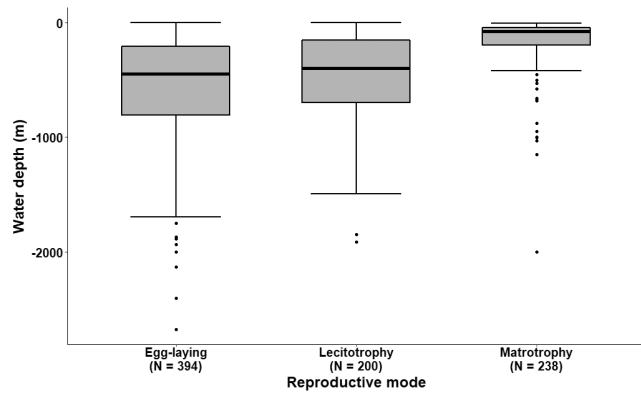


FIGURE 4 Reproductive mode versus water depth in sharks, rays and chimaeras. *N* refers to the number of species, and asterisk indicates a significant difference. For phylogenetically corrected results see [Table 2](#). In each box plot, the thick middle line, box and whiskers represent the median, interquartile range and the minimum and maximum data range, respectively, and the circles represent outlier data points.

form nurseries), or both (Blackburn, 1999), and the survival of larger offspring can be higher in pelagic habitats lacking shelter for offspring from predators. Considering the energetic costs of reproduction, live-bearing could be more adaptive in environments where food availability is not constant, as females can control the flow of the nutrients and even reabsorb the embryos if there is not enough food (Buddle et al., 2019). In contrast, egg-laying species must produce all of the nutrients for the offspring in advance; thus, those resources are lost to the females.

The diversity of reproductive modes was decimated throughout the vertebrate phylogeny. In Chondrichthyes, we have seen that there are five distinct modes of reproduction. By contrast, in most other vertebrates there are two: they are predominantly either oviparous or have placental viviparity, with a few species being ovoviviparous. In their distant evolutionary past, spreading to new habitats, such as when moving to land from the oceans, boosted the evolution of diverse reproductive modes (Vági et al., 2022). However, once these new habitats were settled, efficient solutions for reproduction such as amniotic eggs or placental viviparity might have been favoured and canalized in successful vertebrate clades, thus reducing this temporarily broader repertoire of reproductive modes. Body temperature regulation could also have played a key role in the evolution of reproductive modes: for instance, viviparity, common among mammals, could have arisen in conjunction with them evolving endothermy (Balshine, 2012; Reynolds et al., 2002).

One main limitation of our study is that we may have missed important ecological associations due to the relatively coarse categorisation of habitats. Although we showed here the coevolution of reproductive modes and habitats, future studies are needed to investigate causation: whether habitat changes induced transitions between reproductive mode, or if it is the transitions that enabled sharks and rays to colonize new habitats (Compagno, 1990; Mull et al., 2019; Sorenson et al., 2014). Environmental conditions

have already been shown to affect the evolution of reproductive modes in other vertebrates, e.g., squamate reptiles, anuran and urodelan amphibians (Recknagel et al., 2021; Vági et al., 2020, 2022). It would be interesting to investigate if the emergence of live-bearing and matrotrophy were also associated with paleoclimatic changes. This would allow us to extrapolate the effects of current oceanic climate change on species with various reproductive strategies, an important question in the current context of rapid, human-induced climate change. Finally, since data on life history is still missing for many species, future studies with an even broader taxonomic coverage and/or higher resolution data may uncover additional associations between life history and reproductive modes.

In conclusion, our comprehensive analysis found that in Chondrichthyes different modes of live-bearing with maternal input evolved independently, mostly from an intermediate state of yolk-only viviparity, but also with rapid changes directly from egg-laying. Reproductive mode was also associated with life-history variables including body size, longevity and offspring size. Furthermore, our analysis consistently suggested that live-bearing in ancestral sharks and rays played an important role in their successful radiation into pelagic habitats, transforming several species into the charismatic keystone species and apex predators we know today.

AUTHOR CONTRIBUTIONS

Gergely Katona: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Flóra Szabó:** Formal analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Zsolt Végvári:** Conceptualization, Methodology, Formal analysis, Writing – Review & Editing, Supervision. **Tamás Székely Jr.:** Writing – Review & Editing. **András Liker:** Methodology, Writing – Review & Editing. **Robert P. Freckleton:** Methodology, Writing – Review & Editing. **Balázs Vági:** Conceptualization, Methodology, Writing – Review & Editing, Visualization, Supervision. **Tamás Székely:** Conceptualization, Methodology, Writing – Review & Editing, Supervision.

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CONFLICT OF INTEREST STATEMENT

The authors have declared that no competing interests exist.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All relevant data are within the paper and its electronic Data S1–S3 and are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3j9kd51m8>

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