Maternal investment evolves with larger body size and higher diversification rate in sharks and rays

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Running head: Reproductive Diversification of Sharks

Summary

Across vertebrates, live-bearing has evolved at least 150 times from ancestral egg-laying into a diverse array of forms and degrees of prepartum maternal investment.[1,2] A key question is how this reproductive diversity arose and whether reproductive diversification underlies species diversification?[3–11] To test these questions, we evaluate the most basal jawed vertebrates, sharks, rays, chimaeras of Class Chondrichthyans, which have one of the greatest ranges of reproductive and ecological diversity among vertebrates.[2,12] We reconstructed the sequence of reproductive mode evolution across a time-

calibrated molecular phylogeny of 610 chondrichthyans.[13] We find egg-laying is ancestral, and live-bearing evolved at least seven times. Matrotrophy (i.e. maternal contributions beyond the yolk) evolved at least 15 times, with evidence of one reversal. In sharks, transitions to live-bearing and matrotrophy are more prevalent in larger-bodied species in the tropics. Further, the evolution of live-bearing is associated with a near-doubling of the diversification rate, but, there is only a small increase in diversification associated with the appearance of matrotrophy and increased rates of speciation are associated with the colonization of novel habitats, contrary to what has been demonstrated in teleosts.[3,4] This highlights a potential key difference between chondrichthyans and other fishes, specifically a slower rate of reproductive isolation following speciation, suggesting different rate-limiting mechanisms for diversification between these clades.[14] The chondrichthyan diversification and radiation, particularly throughout the shallow tropical shelf seas and oceanic pelagic habitats, appears to be associated with the evolution of live-bearing and the proliferation of a wide range of maternal investment in developing offspring.

Keywords: Viviparity; parent-offspring conflict; Genomic conflict; Shark; Trait Evolution; placenta; matrotrophy

Results and Discussion

We reveal the first chondrichthyan was an egg-layer and there have been numerous transitions toward live-bearing and matrotrophy (Figure 1). The evolution of live-bearing and matrotrophy covaries with increasing body size and is more prevalent in shallow waters of tropical latitudes (Figure 2). Further, the evolution of live-bearing, and to a lesser extent matrotrophy, appears to have resulted in greater species diversification (Figure 3,4). Next we unpack these findings by considering three questions: What is the sequence of reproductive mode evolution? What ecological factors have driven the evolution of live-bearing and matrotrophy? Is chondrichthyan speciation and diversification explained by viviparity-driven conflict or by novel ecological opportunity?

The sequence of reproductive mode evolution

The first chondrichthyans almost certainly laid eggs, as there is a high level of support for egg-laying (oviparity) as the ancestral state of reproductive mode in chondrichthyans (>99% probability; Figure 1A; see Supplementary Table 1 for a full description of each reproductive mode). There are multiple independent origins of live-bearing (seven) and matrotrophy (15), at a range of taxonomic levels from the superordinal to subgeneric level, with few instances of reversals (one reversal from matrotrophy to lecithotrophic live-bearing; Figure 1B-D). Specifically, live-bearing appears to have evolved from egg-laying at: (a) base of Rhinopristiformes and Myliobatiformes, (b) base of Squalomorphii, (c) base of clade encompassing Brachaeluridae,

74 Orectolobidae, and Rhincodontidae, (d) base of Ginglymostomatidae, (e)
75 within the genus *Bythaelurus*, (f) in *Galeus polli*, and (g) basal to clade
76 encompassing Pseudotriakidae, Triakidae, Hemigaleidae, and
77 Carcharhinidae (Figure 1A). We found no evidence of reversals from live-
78 bearing to egg-laying (Figure 1B). Previous analyses of reproductive evolution
79 in chondrichthyans came to this conclusion based on the available
80 morphological phylogenetic hypotheses, that incorrectly inferred that rays
81 (and skates) as a highly derived group within the Squalimorph sharks[15], but
82 the emerging consensus from molecular data is that rays and sharks are
83 sister taxa.[13,16] With this new molecular tree, we find transitions in
84 reproductive mode are generally toward live-bearing or matrotrophy though
85 this not a strictly linear progression as reversals are infrequent though
86 plausible. We expect that improved biological sampling and phylogenetic
87 reconstructions may yield further examples, particularly in groups displaying
88 subgeneric transitions that are currently poorly phylogenetically resolved (e.g.
89 within catsharks, Scyliorhinidae) or among reproductive modes which may be
90 difficult to differentiate, such as mucoid histotrophy (Table S1).
91 We find no support for live-bearing being ancestral nor evidence of a high
92 rate of reversals to egg-laying from live-bearing that this would necessitate,
93 as suggested previously.[17] Interestingly, a similar controversy has occurred in
94 squamates, a group with highly labile reproductive modes. The most likely
95 model suggested an early origin of viviparity with a high rate of reversals[18],
96 though this result has been questioned based on the choice of phylogenetic

hypotheses and morphological features of live-bearing lineages.[1,19,20] Consequently, support remains for the conventional hypothesis that the ancestral state was oviparity.[20] Live-bearing chondrichthyans, particularly lecithotrophic live-bearers, develop within an egg envelope or candle which is similar to, but thinner than, that found in egg-laying species.[12,21] This retention of the morphological machinery for egg production could make reversals to egg-laying feasible, and may allow for some of the subgeneric reproductive diversity seen within catsharks (Scyliorhinidae). But these data, along with the emerging consensus in reptiles, suggests that egg-laying is the ancestral vertebrate condition – colloquially the egg came before the chicken.

Matrotrophy appears to have evolved independently from lecithotrophic live-bearing at least 15 times with one reversal: (a-c) one to three origins within guitarfish and wedgefish (Rhinopristiformes), (d) basal to stingrays (Myliobatiformes), (e-f) one to three origins within sleeper sharks (Somniosidae), (g) great lanternsharks (*Etmopterus princeps*), (h) tawny nurse shark (*Nebrius ferrugineus*), (i) mackerel sharks (Lamniformes), (j) Pseudotriakidae, (k-m) one to three origins within houndsharks (Triakidae), and (n) base of requiem sharks (Carcharhinidae; Figure 1A). There was evidence of a single instance of reversal from matrotrophy to lecithotrophic live-bearing in the sharptooth houndshark (*Triakis megalopterus*). Overall transitions from egg-laying to live-bearing and to matrotrophy occurred at higher rates then reversals across all partitions that contained multiple reproductive modes (Figure 1C,D)

Transitions between matrotrophic modes can also occur, for example in hound sharks (Family Triakidae) muccoid histotrophy can be used in lieu of, or in concert with, placentotrophy[22] – resulting in intergeneric reproductive diversity.[23] Similarly, lecithotrophic live-bearing and some forms of matrotrophy, particularly muccoid histotrophy found in Rhinopristiformes and some sharks, may not represent discrete character states but rather a continuum that will be revealed only with more detailed histological work in this lineage. Muccoid histotrophy can be difficult to distinguish due to a paucity of uterine morphological specializations and accurate measurements of ash-free dry weight of embryos and ova. In several species of squaliform sharks the change in organic mass from ovum to embryo has been used to identify muccoid histotrophy[24,25], though there is uncertainty given the exact threshold value of change in mass that should be used to distinguish between modes.[26] Thus, large groups predominantly composed of lecithotrophic live-bearing species (i.e. Rhinopristiformes, Squalimorphii) may actually contain a greater diversity of maternal investment than currently measurable or dealt with in this analysis, and future analyses may reveal a greater number of transitions or more accurately define these currently discrete characters along a quantitative gradient of matrotrophic contribution. Despite this uncertainty, chondrichthyans still exhibit remarkably labile reproductive modes compared with other vertebrate groups, more similar to the transition rates seen in the much larger clade Squamata (~10,000 species with >150 origins of live-bearing and 6 origins of matrotrophy).[1]

Evolutionary covariation of reproductive mode

In sharks, live-bearing and maternal investment has covaries with larger body size, tropical latitudes, and increasing latitudinal range, while there is little evidence of covarying with depth.

(1) Live-bearing and matrotrophy evolve with increasing maternal size

Reproductive mode was related to body size, such that larger bodied species had a higher probability of live-bearing and matrotrophic investment (Figure 2A). We found positive covariation with body size, using the threshold model to test for evolutionary covariance between discrete values of reproductive mode and continuous ecological traits, (median = 0.16, 95% CI = 0.09 to 0.22; Effective Sample Size = 3351) indicating transitions in reproductive mode are more prevalent in lineages with larger body size (Figure 2A). The relationship with larger body size was slightly stronger for the transition from egg-laying to live-bearing (0.37 [0.17 to 0.55]; ESS = 3332) than for lecithotrophy to matrotrophy (0.3 [0.14 to 0.48]; ESS = 3600). We speculate that body size may, in effect, be capturing allometric differences in predation pressure and access to food resources, which have been hypothesized as drivers of reproductive evolution in smaller more tractable freshwater livebearers[6,27,28]. Improved foraging ability associated with increasing body size may also allow for transitions to greater degrees of maternal investment as matrotrophic forms of reproduction, particularly

166 histotrophy and placentotrophy present greater demand for consistent
167 energetic intake on mothers.[29,30] We hypothesize that infrequent episodic
168 predation and scavenging in deep sea species may preclude matrotrophy
169 which are predominantly egg-laying or lecithotrophic live-bearing.[29] One
170 prediction based on food limitation would be that matrotrophic females could
171 alter offspring size or number in response to food availability. While we see
172 evidence of litter manipulation in chondrichthyans[31], the opposite has been
173 demonstrated in teleosts.[32] It seems that, in chondrichthyans at least, the
174 origin of live-bearing necessitates an increase in body size to accommodate
175 retained embryos throughout gestation in limited internal body space, if larger
176 offspring size is optimal say due to elevated predation risk in the tropics.[33] As
177 a result, lecithotrophic live-bearing sharks typically have fewer, but larger,
178 pups that are presumably subject to less predation pressure and juvenile
179 mortality.[12,29,34]
180
181 *(2) Live-bearing and matrotrophy evolve in wide-ranging tropical species*
182 *at low latitudes*
183 Live-bearing species are more prevalent in the tropics, specifically
184 transitions from egg-laying to live-bearing are more prevalent in lineages at
185 lower latitudes (minimum latitude: -0.68 [-1.25 to -0.01], ESS = 2915, Figure
186 2C; median latitude: -0.46 [-0.9 to -0.03]; ESS = 3189; Figure 2D). However,
187 there was little evidence that transitions in reproductive mode are related to
188 either median latitude (-0.06 [-0.16 to 0.04], ESS = 3600) or median depth

(0.06 [-0.04 to +0.15]; ESS = 3600; Figure 2 B,D). Transitions to live-bearing and in reproductive mode were more prevalent in lineages with larger latitudinal ranges (0.058 [0.08 to 1.0], ESS = 2580; 0.11 [0.04 to 0.18], ESS = 3956; Figure 2E). Despite detecting a relationship between reproductive mode and body size and latitude in extant chondrichthyans[29], our ability to test for evolutionary covariation is hindered by the phylogenetic clustering of traits and the use of depth and latitude as proxies for environmental temperature and resource availability. As a result, it is currently difficult to disentangle evolutionary hypotheses, as large lineages with similar character states may reflect a single origin and subsequent coinheritance rather than a functional evolutionary covariation.[35] Rays exhibit an interesting transition – consistent with the relationship we have revealed in sharks – from deep cold-water egg-laying skates (either found deep in the tropics or throughout depths in temperate and polar waters) to shallow shelf and coastal live-bearing lineages, including: electric rays (Torpediniformes), guitarfishes, wedgefishes, and sawfishes (Rhinopristiformes), and matrotrophic stingrays (Myliobatiformes). However, our power to test for plausible correlations between reproductive evolution and depth or latitude due to thermal physiology[36], predation[37], and productivity[29] are limited because the batoid lineage contains a single origin of live-bearing and only one certain origin of matrotrophy. Nevertheless, tropical rays (*Himantura* spp.) paradoxically have much slower maximum population growth rates than predicted based on metabolic theory, possibly due to their large relative offspring which are

212 thought to have evolved in response to predation risk. In turn the evolution of
213 large offspring would only be possible through the evolution of maternal
214 gigantism in tropical rays.[39]
215
216 *Viviparity-driven conflict versus novel ecological opportunity*
217 Overall, the evolution of live-bearing and matrotrophy is associated with
218 relatively greater diversification (Figure 3A-C), mainly due to a high relative
219 extinction rate in egg-laying species (Figure 3A,B). The evolution of
220 matrotrophy is associated with greater diversification than egg-laying (2.4
221 times), and there is weak evidence for greater diversification than
222 lecithotrophic live-bearing lineages (1.27 times; Figure 4A). Egg-laying
223 lineages have high turnover driven by high extinction rates because
224 speciation rate is greatest in egg-laying lineages (mean 0.046 lineages/MY)
225 compared with lecithotrophic live-bearing (mean 0.03 lineages/MY) and
226 matrotrophic lineages (0.026 lineages/MY; Figure 3A-C).
227 Within the three radiations, the connection between reproductive mode
228 and diversification is more nuanced. Within the requiem sharks
229 (Carcharhiniformes), egg-laying lineages have a greater diversification rate
230 than lecithotrophic live-bearing lineages (Figure 3D-F, Figure 4B), driven by
231 high speciation in egg-laying cat sharks that are found mainly in deepwater.
232 The “viviparity driven conflict” hypothesis predicts an increase is speciation
233 associated with the evolution of matrotrophy, specifically placentation, as this
234 provides a potential arena for genomic conflict between parent and offspring

235 during pregnancy. This genomic conflict can drive sexual selection and
236 increase the evolution of pre- and postcopulatory reproductive isolation.[5] In
237 poecilid fishes, increased rates of speciation are associated with pre-
238 copulatory mechanisms, specifically male sexually selected traits, while post-
239 copulatory mechanism (i.e. the placenta) had no effect on speciation.[3]
240 Likewise, we did not find support for differences in speciation associated with
241 reproductive modes (Figure 4 A,D). Chondrichthyans do not exhibit male
242 sexually selected traits, yet there is mounting evidence of post-copulatory
243 mechanisms of sexual selection in sharks such as cryptic female choice and
244 possible superfetation.[31,38] This is a notable contrast to other fishes, and may
245 highlight a slower rate of reproductive isolation following speciation in
246 chondrichthyans as pre- and post-copulatory mechanisms of reproductive
247 may not be the rate limiting factor for speciation.[14] Reproductive isolation may
248 be less pronounced in chondrichthyans, and indeed chondrichthyans lack
249 secondary sexual characteristics (such as behavior, dichromatisms, and
250 ornamentism), and there is increasing evidence of viable offspring in
251 congeners.[40–43] Instead novel ecological opportunities appear to be a stronger
252 driver.
253 Across chondrichthyans there appears to be evidence that radiations into
254 novel habitats rather than of reproductive mode generally affects
255 diversification rates, such as into cold water[44] or novel and highly dynamic
256 fragmented freshwater habitats.[45–47] Notably, speciation is particularly high in
257 both the skate radiation (0.078 lineages/MY; Figure 3G) and the South

258 American freshwater stingray radiation (0.070 lineages/MY; Figure 3J),
259 potentially reflecting their colonization of novel polar/temperate shallows and
260 tropical deep-water and freshwater habitats, respectively. While genomic or
261 conflicts or sexual selection may be stronger drivers of speciation in teleosts,
262 they are likely a weak driver of speciation compared to ecological forces
263 across chondrichthyans.

264 The elevated diversification rates seen in skates (Rajiformes), South
265 American Freshwater stingrays (Potamotrygonidae), and ground sharks
266 (Carcharhiniformes) appear to be related to colonization of new ecological
267 space. However, in each case, the ecological space is different – skates
268 radiated into coldwater (polar/temperate shallows and tropical deepwater)
269 habitats with the opening up of the Atlantic Ocean[48], subsequent isolation of
270 ocean basins[49], limited egg and adult dispersal ability[48], and a high degree of
271 spatial niche differentiation.[50,51] By contrast the Neotropical potamotrygonid
272 stingrays (and other fish lineages) colonized freshwater upon the closure of
273 the isthmus of Panama[45,46,52,53], radiating into novel and highly fragmented
274 freshwater habitat potentially facilitated by the emergence of unique
275 morphological adaptations.[54] The increased diversification in ground sharks is
276 driven by both reinvasion of deepwater by catsharks (Scyliorhinidae) and
277 speciation in endemic hotspots, such as South Africa, and the colonization of
278 shallow water coastal habitats (coral reefs and associated inshore and
279 estuarine habitats) by requiem sharks (Carcharhinidae).[44] At present, the
280 weight of evidence suggests that clade-specific increases in diversification

281 rate are associated with new ecological space, rather than being
282 systematically driven by reproductive evolution *per se* – nevertheless, we
283 await stronger tests of this hypothesis when more extensive phylogenies
284 become available. Future investigations of genomic conflict-driven speciation
285 may require refined measurements of ecological variation[55] or life history[56] as
286 drivers of diversification with tests restricted to smaller groups.
287
288 *Conclusions*
289 The evolution of chondrichthyan reproductive modes, ranging from egg-
290 laying to live-bearing and matrotrophy, appears strongly related to body size
291 and temperature-related biogeography. While patterns of species
292 diversification in three major radiations appear to be more strongly driven by
293 colonization of novel habitats in contrast to teleosts, the evolution of the
294 diversity of reproductive modes remains a fruitful area of research. Parent-
295 offspring conflict over resources during development and subsequent
296 antagonistic coevolution is an intriguing potential driver of reproductive mode
297 evolution worthy of further investigation through genomic methods. In
298 particular, the apparent slow evolution of reproductive isolation following
299 speciation, in contrast to other fishes, hints at a different mechanism
300 ultimately regulating the rate of speciation between shark and ray clades.
301 Chondrichthyans are an ideal group to test for this given the diversity of
302 reproductive modes and the frequency of polyandry, though this requires a
303 better understanding of maternal-fetal interactions across a wider range of

species.[31] Future research could focus on improved measures of maternal investment, particularly for identifying the continuum on which lecithotrophic live-bearing and histotrophic matrotrophy may be expressed. Combined with further refinement of phylogenetic hypotheses with more extensive taxon sampling will help to clarify patterns of energetic investment, the degree of income breeding in live-bearing species, and inter- and intra-specific plasticity. More generally, we anticipate that this taxon will yield profound insights into the interplay between reproductive life history evolution, ecology, and the biogeographic patterning of species diversity across the Earth's oceans.

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Author Contributions

CGM, KEY and NKD conceived the study; CGM and MWP designed the analytical approach; CGM performed the analyses; CGM, MWP, KEY and NKD drafted the manuscript. All authors gave final approval for publication.

Declaration of Interests

We have no competing interests.

Inclusion and Diversity

We support inclusive, diverse, and equitable conduct of research.

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RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Christopher Mull (Chris.Mull@dal.ca).

Materials Availability

Phylogenetic trees have been deposited at http://vertlife.org/sharktree[13], and trait information has been deposited at http://www.sharkipedia.org[57], and are publicly available as of the date of publication, a list of species can be found in the supplementary material.

Data and Code Availability

All phylogenetic trees are available at www.vertlife.org/sharktree.[13] All life history and trait information is available at www.sharkipedia.org.[57]

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethics Statement

No live animals or human subjects were used in this study.

Data Availability

All phylogenetic trees are available at www.vertlife.org/sharktree, and all trait information is available at www.sharkipedia.org.

METHOD DETAILS

Trait Data and Phylogeny

Data on the reproductive mode and habitat type were collected for the 610 chondrichthyan species in our phylogeny, from primary literature and species catalogues.[58–60] Chondrichthyans exhibit eight distinct reproductive modes[2], though we focus the evolution of live bearing and maternal investment, therefore species were categorized into three distinct modes: egg-laying, lecithotrophic live-bearing, and matrotrophic live-bearing where embryos are nourished via the initial yolk-sac investment and additional maternal contributions during gestation (oophagy, histotrophy, and placentotrophy). We note that lecithotrophic live-bearing has also been called yolk-sac viviparity, aplacental viviparity, or ovoviparity.[10] We collected data on maximum body size and depth ranges (minimum, mean, median, and maximum) from species field guides and catalogues and primary literature. Minimum and maximum latitudinal range was collected from species geographic range maps from the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species database.[58,59] Median latitude was calculated as the midpoint between minimum and maximum latitude, and was expressed as an absolute value to represent distance north or south from the equator. All continuous trait values were standardized, centered, and divided by two standard deviations, using the rescale function in the arm (version 1.9-3)[61] package prior to analyses to facilitate comparison of coefficients.

632 We conducted all analyses using a distribution of trees from a new 610
633 species chondrichthyan molecular phylogeny.[13] This phylogeny covers 51%
634 of all known species from every order, 98% of families, 88% of genera, and all
635 described character states are represented. Because the distribution of trees
636 represents a gradient of variation in root and node dating for the maximum
637 likelihood tree, we sequentially selected 21 trees, every 25th tree from one to
638 500 to account for the full range of temporal calibrations. Results were pooled
639 across all trees.
640
641 *Ancestral State Reconstruction and Diversification*
642 We reconstructed the evolutionary origins and sequence of reproductive
643 mode and habitat while estimating state dependent diversification rates using
644 the multistate speciation and extinction (MuSSE) method with maximum
645 likelihood implemented with musse[62] in the diversitree (version 0.9-9)
646 package in R.[63] Rabosky and Goldberg [64] pointed out that state dependent
647 diversification models (including MuSSE) are susceptible to inflated false
648 positives when there is unmodeled heterogeneity in diversification rates –
649 thereby associations can be falsely detected between rates and states even
650 when the diversification dynamics are unrelated to the traits being considered.
651 To minimize false positives, we adopted the analytical approach of Uyeda et
652 al.[65] and integrated a hypothesis-testing approach (i.e., MuSSE) with a more
653 data-driven approach (what Uyeda et al. refer to as “phylogenetic natural
654 history”); in this way, we are able to tease out the signal for our hypotheses

655 that our focal traits are influencing diversification rates while conditioning on
656 the fact that there is likely substantial background variation in these rates
657 across the tree.

658 More specifically, we first used the medusa algorithm (as implemented in
659 Geiger v2.0.6[66] to detect background variation in diversification rates
660 unrelated to our traits of interest. First, we infilled those species missing from
661 the molecular phylogeny (n = 582) using taxonomic constraints so that tips
662 represented unresolved clades. Importantly for earlier divergences, our
663 sampling did not miss any variability in reproductive mode (e.g. there are no
664 live-bearing chimaeras) so missing samples will not affect our conclusions.
665 Under some circumstances, medusa may not reliably correctly identify the
666 placement of shifts.[67] However, this issue does not pertain to our analysis
667 because we are not making any inferences about specific events or specific
668 clades and are only interested in detecting broad-scale differences in
669 diversification dynamics. Our Medusa analysis only revealed three clades
670 with consistent increases in diversification rates across all trees: skates
671 (Rajiformes), South American freshwater stingrays (Potamotrygonidae), and
672 ground sharks (Carcharhiniformes). For the MuSSE analyses, we then
673 partitioned the tree into four diversification regimes (these three known
674 radiations plus the background) and fit a MuSSE model in which the
675 diversification rate parameters were allowed to vary among these four
676 partitions. We also assigned each partition its own sampling fraction based on
677 the most up-to-date taxonomic treatment.[13,68] Ideally, we would have fit an

678 integrated model that included heterogeneity in rates due to both the trait and
679 to unmodeled "background" variation[65,69] but unfortunately no such approach
680 is available for multi-state traits.

681 As we described above, speciation (λ), extinction (μ), and transition rates
682 (*q*) were estimated for each of the four partitions separately. Because the
683 estimations of extinction rates from molecular phylogenies can be difficult[70],
684 we ran two models: with state dependent extinction rates (1) unconstrained
685 ($\mu_{egg\text{-}laying} \neq \mu_{live\text{-}bearing} \neq \mu_{matrotrophic}$) and (2) constrained to be equal ($\mu_{egg\text{-}laying}$ =
686 $\mu_{live\text{-}bearing} = \mu_{matrotrophic}$). We report findings from the unconstrained model as
687 there was no significant difference between models, and we are interested in
688 how variation in this rate may affect overall diversification. Additionally, the
689 main difficulty with estimating extinction rates arises from unaccounted for
690 diversification rate heterogeneity, which we have minimized by *a priori*
691 identification with medusa and subsequent partitioning. We report speciation
692 (λ), extinction (μ), net diversification ($r = \lambda - \mu$), and transition rates (*q*). We
693 treated reproductive mode as an ordinal multistate character and accordingly
694 did not allow unlikely transitions such as directly between egg-laying and
695 matrotrophic live-bearing. Models were run for 10,000 generations with the
696 first 1,000 generations discarded as burn-in, using an exponential prior with a
697 rate of $1/(2r)$ where *r* is the character state independent diversification rate.[63]
698 We checked that all parameter estimates had effective sample sizes (ESS:
699 the number of independent draws from an MCMC chain) greater than 200. To
700 account for autocorrelation in the estimates of state dependent diversification,

701 we also examined the posterior distribution of differences in state dependent
702 rates across all chains.
703
704 *Evolutionary Covariation with Ecological Traits*
705 We used a threshold model to test for the evolutionary covariation
706 between reproductive mode and continuous ecological traits. The threshold
707 model assumes that state changes in an ordinal variable (e.g. egg-laying to
708 live-bearing to matrotrophy) occur when a threshold value of an underlying
709 continuous latent variable, such as body size, is reached. Thus, it can be
710 used to model the evolutionary covariation between ordinal and continuous
711 traits.[71] Accurate estimation of evolutionary covariation requires a suitable
712 number of transitions and distribution of traits across the phylogeny.[35] We
713 focus on sharks (superorders Galeomorphii and Squalomorphii; n = 292) to
714 evaluate evolutionary covariance between reproductive transitions and three
715 ecological traits (body size, depth, and latitude), because there is only one
716 transition in parity and few appearances of matrotrophy within
717 Chimaeriformes and rays (Batoideii). We estimated the evolutionary
718 covariance using Bayesian methods, sampling from the posterior distribution
719 using a special Reduced Animal Model implemented in a mixed effects
720 modeling framework while accounting for phylogeny, using the package
721 MCMCglmmRAM (version 2.24) in R.[72] This approach is equivalent to
722 estimating evolutionary covariance using the threshold model.[71,73] These
723 models are a special case of generalized linear mixed effects models where

724 heritability, akin to Pagel's λ, is set to a value of one corresponding to
725 Brownian motion with respect to the phylogenetic tree.[74,75] Twenty chains
726 were run for 2 million generations with the first 200,000 iterations discarded
727 as burn-in, using priors with an inverse-Wishart distribution and the residual
728 covariance matrix set to zero.[72] Samples were drawn every 500 iterations to
729 avoid temporal autocorrelation in parameter estimates. Chains were visually
730 inspected to ensure convergence using coda (version 0.19-4)[76], and posterior
731 samples were summarized to generate mean and 95% highest posterior
732 densities (HPD) with effective samples sizes greater than 1000. Models were
733 run using three different treatments of reproductive mode with the threshold
734 family: binary parity mode (egg-laying versus live-bearing), binary embryo
735 trophic mode (lecithotrophic versus matrotrophic), and ordinal multi-state
736 reproductive mode (egg-laying, lecithotrophic live-bearing, and matrotrophic
737 live-bearing).

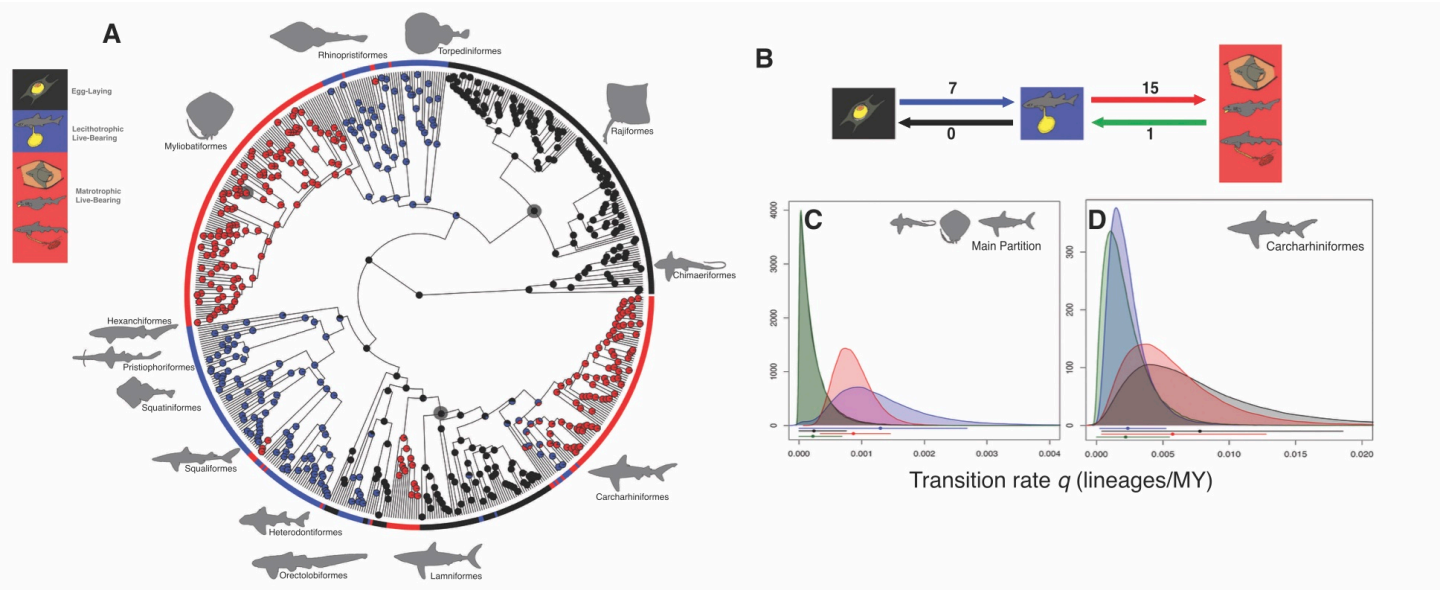
Figure Legends

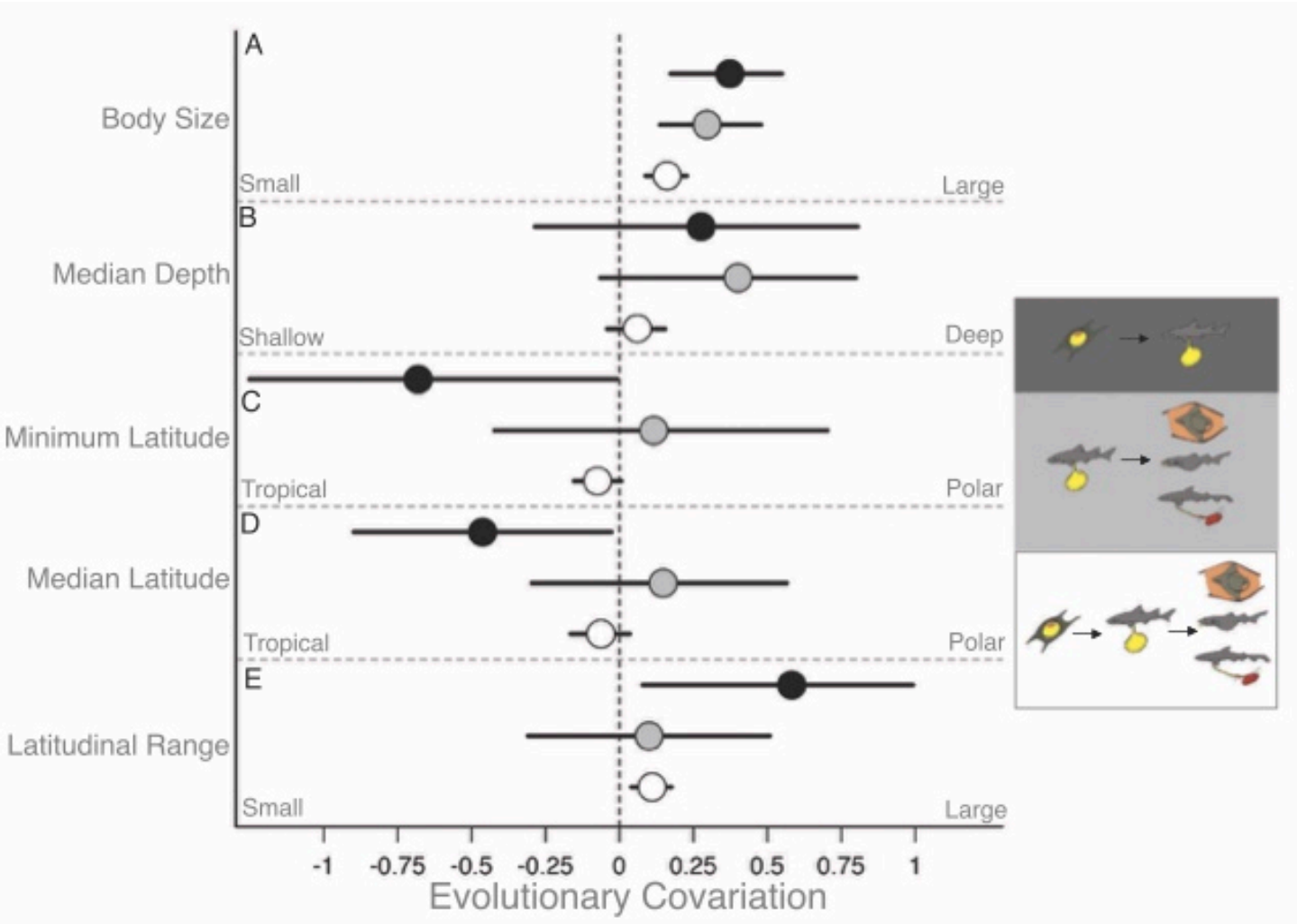
Figure 1. (A) Ancestral state reconstruction reproductive mode on a representative tree of 610 species of chondrichthyans. Pie symbols represent the likelihood of the character state for each node being egg-laying (black), live-bearing (blue), or matrotrophic (red). Dark grey symbols denote the partitions encompassing diversification rate shifts. Silhouettes depict representative species from the major orders. (B) The number evolutionary transitions in reproductive mode across chondrichthyans and transition rates between modes in (C) main partition of the tree and (D) within Carcharhiniformes. Origins of live-bearing from egg-laying are depicted in blue with reversals in black, and origins of matrotrophy from lecithotrophic live-bearing are depicted in red with reversals in green. Bars and shaded regions in represent the 95% posterior density of transition rate estimates.

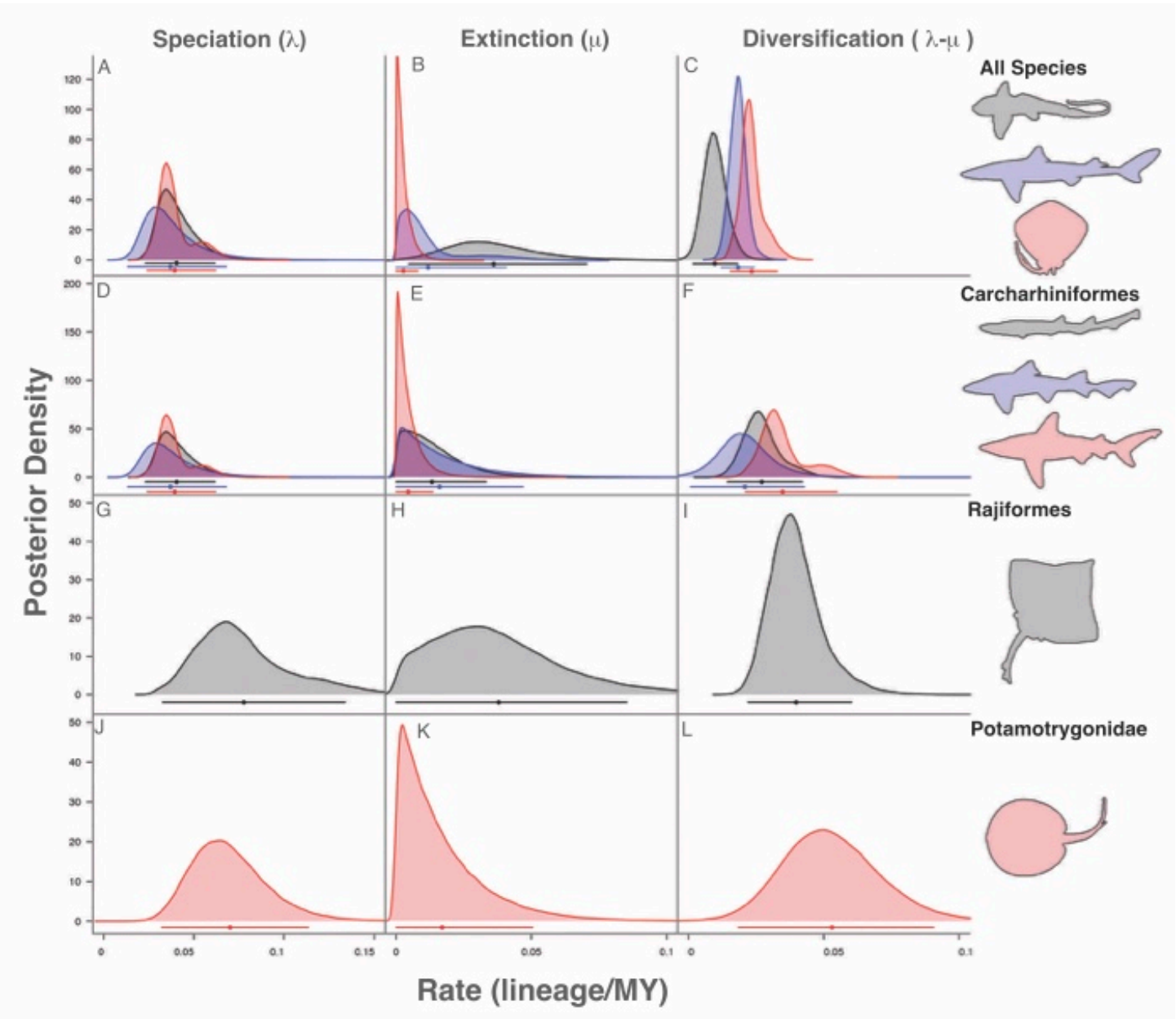
Figure 2. Coefficient plots of evolutionary covariation between (A) body size, (b) median depth, (c) minimum latitude, (d) median latitude, and (e) latitudinal range from MCMCglmm models. Black circles denotes egg-laying vs. live-bearing, grey circles denote live-bearing vs matrotrophy, and open circles denote reproductive mode as an ordinal variable with all three character states. Horizontal bars represent the 95% confidence intervals of the mean posterior estimate.

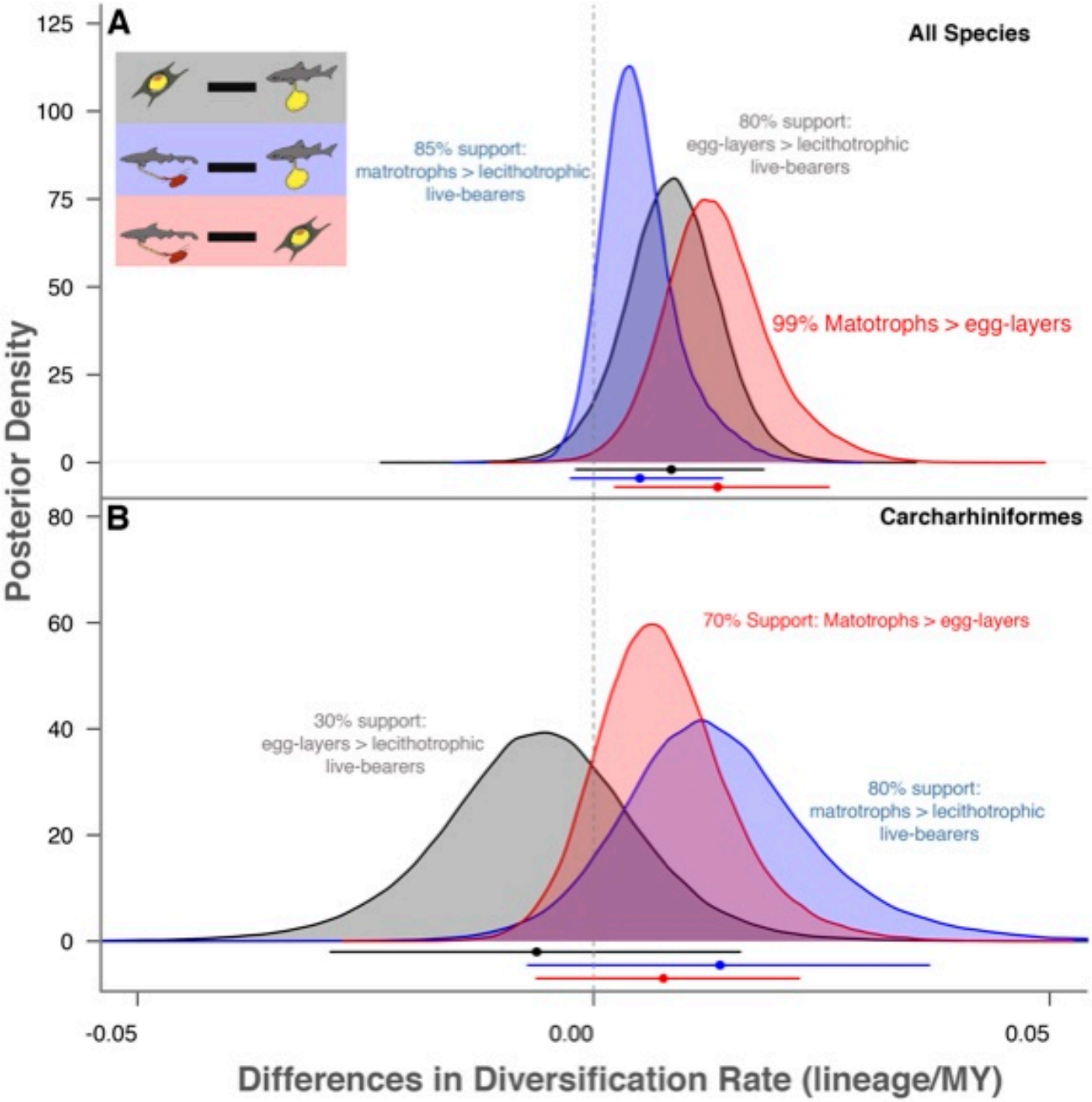
Figure 3. Posterior densities of parameter estimates from MuSSE model showing state dependent speciation (λ), extinction (μ), and net diversification rate (*r*) from the main partition of the tree (A-C), within the order Carcharhiniformes (D-F), within the order Rajiformes (G-I), and within the family Potamotrygonidae (J-L). Egg-laying is depicted in black, live-bearing in blue, and matrotrophy in red. Bars and circles represent the mean and 95% confidence interval of the posterior mean estimate.

Figure 4. Differences between posterior densities of parameter estimates from MuSSE model showing the differences in reproductive mode dependent net diversification rates (*r*) from the main partition of the tree (A), and within the order Carcharhiniformes (B). Live-bearing relative to egg-laying is depicted in black, matrotrophy relative to live-bearing in blue, and matrotrophy relative to egg-laying in red. Bars and circles represent the mean and 95% confidence interval of the posterior mean estimate. The vertical lines denote no difference between the diversification rates for the reproductive modes being compared.


A
Egg-Laying
Lecithotrophic Live-Bearing
Matrotrophic Live-Bearing
Rhinopristiformes
Torpediniformes
Myliobatiformes
Rajiformes
Chimaeriformes
Hexanchiformes
Pristiophoriformes
Squatiniformes
Squaliformes
Carcharhiniformes
Heterodontiformes
Orectolobiformes
Lamniformes
B
7
0
15
1
C
Main Partition
D
Carcharhiniformes
Transition rate q (lineages/MY)


A
Body Size
Small
Large
B
Median Depth
Shallow
Deep
C
Minimum Latitude
Tropical
Polar
D
Median Latitude
Tropical
Polar
E
Latitudinal Range
Small
Large
-1
-0.75
-0.5
-0.25
0
0.25
0.5
0.75
1
Evolutionary Covariation


Speciation (λ)
Extinction (μ)
Diversification (λ-μ)
A
B
C
D
E
F
G
H
I
J
K
L
All Species
Carcharhiniformes
Rajiformes
Potamotrygonidae
Posterior Density
Rate (lineage/MY)


A
All Species
85% support:
matrotrophs > lecithotrophic
live-bearers
80% support:
egg-layers > lecithotrophic
live-bearers
99% Matotrophs > egg-layers
B
Carcharhiniformes
70% Support: Matotrophs > egg-layers
30% support:
egg-layers > lecithotrophic
live-bearers
80% support:
matrotrophs > lecithotrophic
live-bearers
Posterior Density
125
100
75
50
25
0
80
60
40
20
0
-0.05
0.00
0.05
Differences in Diversification Rate (lineage/MY)