

# Life-history correlates of the evolution of live bearing in fishes

Nicholas B. Goodwin<sup>1</sup>, Nicholas K. Dulvy<sup>2</sup> and John D. Reynolds<sup>1\*</sup>

<sup>1</sup>*School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK*

<sup>2</sup>*Department of Marine Sciences, University of Newcastle upon Tyne, Newcastle upon Tyne NE1 7RU, UK  
(n.k.dulvy@ncl.ac.uk)*

Selection for live bearing is thought to occur when the benefits of increasing offspring survival exceed the costs of reduced fecundity, mobility and the increased metabolic demands of carrying offspring throughout development. We present evidence that live bearing has evolved from egg laying 12 times in teleost (bony) fishes, bringing the total number of transitions to 21 to 22 times in all fishes, including elasmobranchs (sharks and rays). Live bearers produce larger offspring than egg layers in all of 13 independent comparisons for which data were available. However, contrary to our expectation there has not been a consistent reduction in fecundity; live bearers have fewer offspring in seven out of the 11 available comparisons. It was predicted that live bearers would have a larger body size, as this facilitates accommodation of developing offspring. This prediction was upheld in 14 out of 20 comparisons. However, this trend was driven by elasmobranchs, with large live bearers in seven out of eight comparisons. Thus, while the evolution of live bearing in elasmobranchs is correlated with predicted increases in offspring size and adult size, teleost live bearers do not have such a consistent suite of life-history correlates. This suggests that constraints or selection pressures on associated life histories may differ in live-bearing elasmobranchs and teleost fishes.

**Keywords:** comparative method; reproduction; viviparity; phylogeny; shark; coelacanth

## 1. INTRODUCTION

Live bearing has evolved from egg laying in a large number of diverse taxa, in terrestrial, marine and freshwater environments (Wourms 1981, 1994; Shine 1983, 1989; Clutton-Brock 1991; Blackburn 1992; Dulvy & Reynolds 1997). Live bearing is hypothesized to have evolved as a means of increasing the survival of offspring in several ways. Internal development shields offspring from extremes of temperature, anoxia and osmotic stress as well as predation (Balon 1977; Shine 1978, 1989; Clutton-Brock 1991; Wourms & Lombardi 1992). The offspring of ectotherms such as fishes and reptiles may also benefit from live bearing because adult body temperature remains above ambient temperatures (Fry 1971). This increases the rate of embryonic development (Shine & Bull 1979; Shine 1989) and can enhance offspring survival (Sergeev 1940; Shine 1995). The potential for provisioning offspring internally may allow females to produce larger offspring with a higher rate of survival as a result of advanced feeding, digestion, movement or behaviour (Amoroso 1968; Wourms 1977; Miller 1979; Baylis 1981; Wourms & Lombardi 1992).

Various costs have been proposed which may offset the benefits of live bearing, thereby limiting the occurrence of this reproductive mode. There may be high energetic costs of carrying the young during gestation, as offspring draw

heat and oxygen from their mother (Boehlert *et al.* 1991; Qualls & Shine 1998). In species that provide nutrients to developing offspring, costs also include the development of complex placenta-like structures or uterine secretions (Wourms & Cohen 1975; Wourms 1981, 1993; Dulvy & Reynolds 1997). Live bearing may also reduce a parent's mobility (Fitch 1970; Thibault & Schultz 1978), thereby exposing it to predation. Finally, retention of offspring may increase time between successive broods, particularly in elasmobranchs that retain offspring for months or years.

The costs of live bearing are thought to have been paid through a variety of life-history adaptations to compensate. Growth and reproductive effort in fishes are closely correlated with body size (Duarte & Alcaraz 1989; Elgar 1990; Visman *et al.* 1996; Froese & Binohlan 2000). Body size can constrain the maximum internal volume that offspring can occupy before birth (Qualls & Shine 1995). Therefore, live bearers have been predicted to have evolved one or both of the following: (i) increased parental body size, and (ii) reduced fecundity. While reduced offspring size could also relieve pressures on parental size or fecundity, it has been suggested that the opposite may occur, whereby live bearers evolve larger offspring size to take advantage of enhanced safety for offspring and opportunities for post-zygotic provisioning (Wourms & Lombardi 1992; Qualls & Shine 1995).

The benefits of live bearing are similar to those proposed for egg-laying species that provide parental care, in that both increase the survival of offspring. Thus, Shine & Bull (1979) proposed that parental egg guarding may be an intermediate step in the evolution of live bearing in

\* Author for correspondence (reynolds@uea.ac.uk).

One contribution of 15 to a special Theme Issue on parental care.

lizards and snakes. Analyses by De Fraipont *et al.* (1996) suggested that although some close relatives of live-bearing snakes and lizards guard their eggs, they have evolved independently. However, the strength of this conclusion has been disputed because De Fraipont *et al.* (1996) included poorly resolved species relationships and a biased dataset that underestimated the incidence of egg guarding in the wild (Blackburn 1999; Shine & Lee 1999).

One way to understand the adaptive nature and evolution of live bearing is to make comparisons among taxa of various life-history traits that have been predicted to covary with modes of reproduction. Although trade-offs are experienced by individuals, if the responses to selection are sufficiently strong and general, it may be possible to see them in comparisons among related taxa. First we test for an association between live bearing and large offspring (Wourms & Lombardi 1992). Second, we test whether live bearers produce fewer offspring, as expected from either an increase in offspring size, or space and energy limitations through retention of the embryos (Fitch 1970; Wourms & Lombardi 1992; Qualls & Shine 1995). Third, we test the hypothesis that live-bearing fishes are larger than their most closely related counterparts. Our tests for these predicted life-history correlates of live bearing include comparisons of teleosts with elasmobranchs, to see whether these highly divergent taxa show similar patterns.

## 2. MATERIAL AND METHODS

### (a) *Live bearing in fishes*

Two discrete reproductive categories were examined in our analyses:

- (i) egg laying (or oviparity), where females spawn eggs with no post-zygotic parental input; and
- (ii) live bearing (or viviparity), where females show either leicithotrophy (embryos are nourished with egg-borne nutrients), or matrotrophy (embryos nourished by maternal contributions provided during development) (Wourms 1981, 1994; Dulvy & Reynolds 1997).

To survey the number of transitions between egg laying and live bearing in teleosts, we began with the foundation laid by Wourms (1981, 1994), updated by an extensive literature search, including new phylogenetic revisions (see Appendix A). For elasmobranchs, we used the recent study by Dulvy & Reynolds (1997), which found evidence that live bearing has evolved nine to ten times. Based on the composite phylogeny in that study, we identified nine sister egg-laying and live-bearing taxa for comparison. For each comparison reproductive information was traced onto a group phylogeny using *MACCLADE* v. 3.07 (Maddison & Maddison 1992). The closest pair of egg-laying and live-bearing clades were selected by hand following the example of Maddison (2000; fig. 1). Appendix A shows each phylogenetic comparison with character information and the source of relationships cited. The live-bearing coelacanth, *Latimeria chalumnae* (Sarcopterygii: Coelacanthiformes) was also included and compared to its egg-laying sister clade comprising the lungfishes (Sarcopterygii: Dipnoi) and tetrapods (Sarcopterygii) (Appendix A). The seahorses and pipefishes (Teleostei: Syngnathidae) are not included because they incubate eggs internally in a male brood pouch, which is not directly

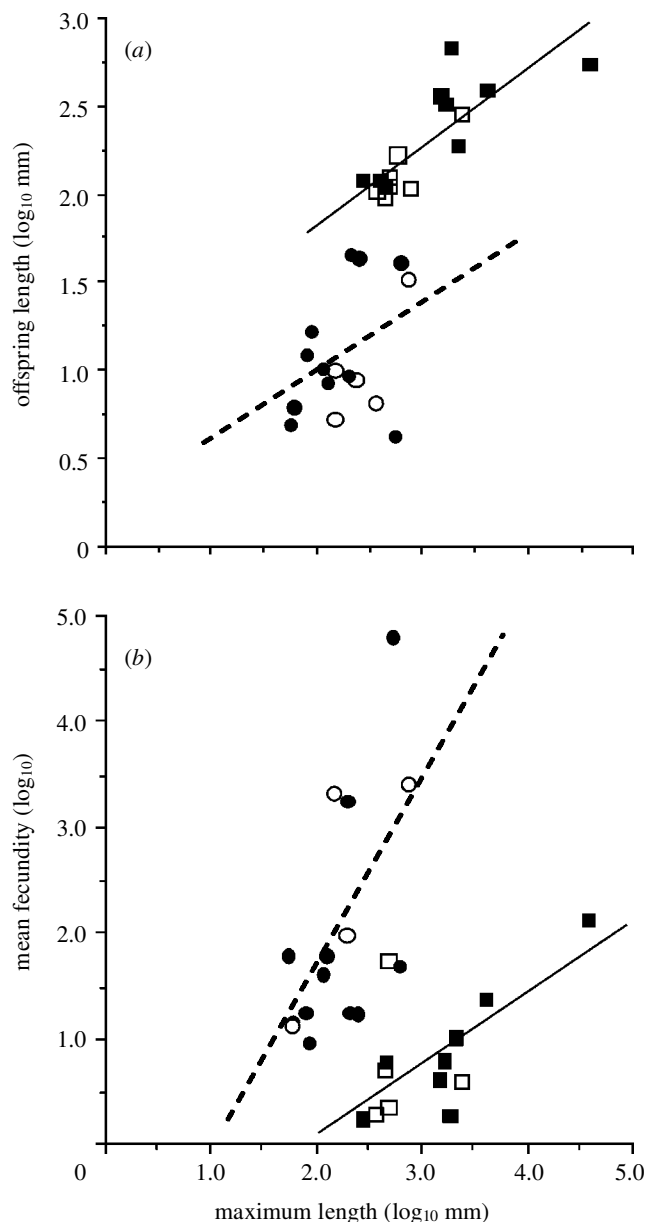


Figure 1. Cross-taxonomic relationships between adult maximum length ( $\log_{10}$ ) and (a) offspring length ( $\log_{10}$ ) ( $n = 32$ ) and (b) mean fecundity ( $\log_{10}$ ) ( $n = 28$ ) in fishes. Each data point represents the nested mean of an egg-laying or live-bearing clade (Appendix A). Regression lines are shown for teleosts (dashed) and elasmobranchs (solid), see text for details. White circles, teleost egg layer; black circles, teleost live bearer; white squares, elasmobranch egg layer; black squares, elasmobranch live bearer.

comparable to female live bearing in other fishes. All other known transitions to live bearing in living fishes are represented.

### (b) *Life-history data*

Data on maximum recorded total length (mm), offspring length (mm) and mean fecundity were taken from key reviews of taxa, primary scientific papers and aquarist literature. There were too few data for comprehensive analyses of female maximum length or asymptotic length, but for those species where data were available, female maximum length did not differ significantly from the maxima recorded for either teleost or elasmobranch species. Eschmeyer (1998) was used to confirm

the validity of species used in the study. Duration of egg development and gestation were not included in analyses because the necessary data concerning both egg size and the temperature of development were not available. Egg size and temperature have strong effects on the development of offspring (Duarte & Alcaraz 1989; Blaxter 1992). The paucity of data available on egg size also precluded analyses of clutch volume.

The number of evolutionary transitions from egg laying to live bearing limits the total sample sizes available for comparison for the different life-history traits (maximum total length,  $n = 20$ ; offspring length,  $n = 13$ ; and mean fecundity,  $n = 11$ ) (Appendix A). Sample sizes within these paired comparisons depended on the species richness of the group and character data available. Not all species have been sampled adequately in the literature. Some species characteristics were taken from original descriptions of single specimens, but other measurements were taken from many specimens of each species. Maximum length was described for 69% of live bearers and 79% of egg layers. However, information on reproductive traits is biased towards live-bearing taxa for offspring length (32% versus 5%), and mean fecundity (20% versus 4%). This limited some analyses through small sample size. Species traits were included regardless of sampling effort. This is the most conservative procedure (Shine 1994). When minimum or maximum trait values were required, the absolute values for each species were taken from the literature. Unless the means were reported they were calculated as the midpoint between the minimum and maximum trait value. We surveyed 1308 species of teleost (731 egg layers and 577 live bearers) and 638 species of elasmobranch (330 egg layers and 308 live bearers) from eight orders and 28 families. The family Latimeriidae consists of one species, the lungfishes include six species and the tetrapods were represented by information from 25 species of Anura (frogs and toads).

### (c) Analysis of life-history characters

Key comparisons were between sister taxa that differed in reproductive mode, i.e. live bearers versus their closest egg-laying relatives. For each egg-laying and live-bearing clade in a comparison a nested mean for each trait was calculated using the taxonomic levels of species, genus and family. Nesting trait values retain variance from the species and generic levels for the higher-level comparisons, and correct for autocorrelation when comparing sister groups. A more exact method is to optimize traits onto a large composite phylogeny. This avoids potential bias when a trait value of a basal lineage differs from the mean trait value derived from the majority of taxa. This approach was not used because of poor knowledge of phylogenetic relationships within clades. Our approach reveals differences between live-bearing and egg-laying sister taxa; however, we cannot draw conclusions about the direction of change. All data were  $\log_{10}$  transformed prior to analysis. Teleost and elasmobranch fishes were treated separately because of differences in absolute size and allometric relationships between maximum length and offspring length and mean fecundity (Wourms & Lombardi 1992; this study). Based on the phylogenetic position of the coelacanth versus lungfish–tetrapod comparison (relative to teleost and elasmobranch fishes), we consider that it is sufficiently different to be treated separately. Therefore the coelacanth, lungfish–tetrapod comparison is included in paired comparisons but not in teleost or elasmobranch regression analyses. A paired-sample sign test using one-tailed  $p$ -values was used to test the predicted differences between egg layers and live bearers under directional hypotheses. Body size limits maximum fecundity, and under

selection for maximum offspring survival we do not expect a reduction in offspring length. Traits were tested with and without controlling for body size. Offspring length and mean fecundity were adjusted for their allometric relationship with maximum length by using relative values taken as residuals from the regression. Residual errors were standardized by dividing them by their expected variance to ensure equality of variances (Zar 1996). Regression and  $t$ -test statistics use the nested mean values for egg layers and live bearers. For maximum length, treating teleosts and elasmobranchs separately gives small sample sizes for a paired-sample test, so for each pair of comparisons the live-bearing value was plotted against the egg-laying value. The difference between the slope of the paired-sample comparison regression line and the null model line of equality (a gradient of unity) was tested following Zar (1996). A significant deviation from this line suggests a functional association between the maximum length and reproductive mode.

## 3. RESULTS

### (a) Transitions to live bearing in fishes

Live bearing occurs in 14 families of bony fishes and we estimate that it has evolved at least 12 times in this group (Teleostomi) (table 1). This reproductive mode is rare, occurring in only 2–3% of teleost species. Taken together with a recent study of elasmobranchs showing that 60% of species are live bearers, due to nine to ten evolutionary transitions (Dulvy & Reynolds 1997), this indicates a total of 21–22 transitions in fishes. Each teleost transition to live bearing forms a monophyletic clade nested among egg-laying outgroups. Therefore live bearing in teleosts is derived from egg laying, and there is no evidence of reversals from live bearing to egg laying.

### (b) Offspring length

There is a weak and statistically non-significant relationship between adult maximum length ( $\log_{10}$ ) and offspring length ( $\log_{10}$ ) for teleosts ( $y = 0.196 + 0.394x$ ;  $r^2 = 0.152$ ;  $t = 1.58$ ; d.f. = 14;  $p = 0.136$ ) (figure 1a), but a strong relationship for elasmobranchs ( $y = 0.945 + 0.444x$ ;  $r^2 = 0.672$ ;  $t = 5.54$ ; d.f. = 14;  $p < 0.0001$ ) (figure 1a). The slopes of the allometric relationships between maximum length ( $\log_{10}$ ) and offspring length ( $\log_{10}$ ) do not differ significantly between teleosts and elasmobranchs ( $t = 0.296$ ; d.f. = 28;  $p > 0.500$ ) (figure 1a). Independent of reproductive mode, elasmobranchs have much larger offspring than teleosts ( $t = 10.72$ ; d.f. = 30;  $p < 0.001$ ) (figure 1a, table 2). The coelacanth has larger offspring than its lungfish–tetrapod sister comparison (320 mm versus 7 mm) (Appendix A).

Live bearers have larger offspring than their egg-laying relatives in all of the 13 comparisons (paired-sample sign test:  $p = 0.0001$ ). When offspring length is considered relative to adult body size, live bearers in 11 out of the 13 comparisons still have larger offspring (paired-sample sign test:  $p = 0.011$ ).

### (c) Fecundity

There is a significant, weak relationship between maximum length ( $\log_{10}$ ) and mean fecundity ( $\log$ ) for the teleosts in our dataset ( $y = -1.948 + 1.822x$ ;  $r^2 = 0.356$ ;  $t = 2.678$ ; d.f. = 13;  $p = 0.019$ ) (figure 1b), and for the elasmobranchs ( $y = -1.249 + 0.677x$ ;  $r^2 = 0.439$ ;  $t = 3.063$ ;

Table 1. Live-bearing families and number of transitions from egg laying to live bearing in bony fishes (Teleostomi). (The number of valid genera and species are based on Eschmeyer (1998).)

taxon	number of transitions	frequency live bearing by genera	frequency live bearing by species
grade Teleostomi (total)	12	135/226	577/1006
class Sarcopterygii			
order Coelacanthiformes			
Latimeriidae (coelacanth)	1	1/1	2/2
class Actinopterygii			
order Beloniformes			
Hemiramphidae (halfbeaks)	1	4/12	26/101
order Cyprinodontiformes			
Anablepidae (four-eyed fishes)	1	2/3	11/12
Goodeidae (Goodeids)	1	17/19	39/43
Poeciliidae (Poeciliids)	1	28/40	208/280
order Ophidiiformes			
Aphyonidae <sup>a</sup>	1	6/6	8/8
Bythitidae <sup>a</sup> (viviparous brotulas)		34/34	51/51
Parabrotulidae <sup>a</sup> (false brotulas)		2/2	2/2
order Perciformes			
Embiotocidae (surfperches)	1	13/13	24/24
Clinidae <sup>a</sup> (kelpfish)	1	21/26	80/89
Labrisomidae <sup>a</sup> (Labrisomids)	1	2/16	15/62
Zoarcidae (eelpouts)	1	1/46	3/221
order Scorpaeniformes			
Comephoridae (baikal oilfishes)	1	1/1	2/2
Sebastidae <sup>a</sup> (rockfishes)	1	3/7	106/109

<sup>a</sup> Families with species or genera that are placed provisionally.

Table 2. Summary of egg-laying and live-bearing life-history character traits for teleost and elasmobranch fishes.

(Minimum and maximum fecundities are absolute values. Two taxa with extreme values of fecundity are excluded (Sebastinae, comparison 10 and *Rhincodon typus*, comparison 17; see Appendix A). When Sebastinae are included the mean fecundity of teleosts =  $47\,695.6 \pm 18\,923.1$  s.e.; and maximum =  $2.7 \times 10^6$ . When *Rhincodon typus* is included the mean fecundity of elasmobranchs =  $9.9 \pm 1.7$  s.e.; and maximum = 300.)

taxon	life-history character	egg laying			live bearing		
		mean ( $\pm$ s.e.)	range	<i>n</i>	mean ( $\pm$ s.e.)	range	<i>n</i>
teleosts	maximum length (mm)	149.9 $\pm$ 7.7	6.5–2000	477	159.9 $\pm$ 8.9	20–1080	443
	offspring length (mm)	11.9 $\pm$ 3.3	2.4–33	9	10.8 $\pm$ 0.8	2–67	196
	mean fecundity	2191.6 $\pm$ 1424.8	10–10531	5	230.4 $\pm$ 130.6	1–4660	79
elasmobranchs	maximum length (mm)	780.4 $\pm$ 33.0	160–2500	167	2125.5 $\pm$ 362.5	185–3600	144
	offspring length (mm)	130.9 $\pm$ 9.9	12–340	40	392.2 $\pm$ 21.8	60–1540	121
	mean fecundity	17.7 $\pm$ 4.9	2–153	35	7.7 $\pm$ 0.6	2–82	116

d.f. = 11;  $p = 0.010$ ) (figure 1*b*). Independent of reproductive mode, teleosts are significantly more fecund than elasmobranchs in absolute terms ( $t = 3.904$ ; d.f. = 26;  $p < 0.001$ ), and they differ in their allometric relationships between body size and fecundity (comparison of slopes:  $t = 2.49$ ; d.f. = 24;  $p = 0.020$ ) (figure 1*b*, table 2). The live-bearing coelacanth has fewer offspring than its lungfish-tetrapod sister comparison (Appendix A). Live bearers are less fecund than their egg-laying relatives in seven out of the 11 comparisons (paired-sample sign test:  $p = 0.274$ ). When fecundity is considered relative to adult body size, one comparison is lost because of missing data for maximum length, and seven out of the ten comparisons show that live-bearing fish are less fecund than their egg-laying relatives (paired-sample sign test:  $p = 0.172$ ).

#### (d) Body size

Fourteen out of the 20 paired comparisons show that live-bearing fishes are larger than their egg-laying relatives (paired-sample sign test:  $p = 0.021$ ). The coelacanth is larger than its lungfish-tetrapod sister comparison (figure 2, Appendix A). Elasmobranchs, which are much larger than teleosts ( $t = 5.617$ ; d.f. = 37;  $p < 0.0001$ ) (table 2), deviate from the null 1:1 line ( $t = 4.051$ ; d.f. = 6;  $p < 0.010$ ) (figure 2). Seven of the eight elasmobranch comparisons show that live bearers are larger than their egg-laying relatives compared with the null model. Live bearers in six of the 11 teleost comparisons are larger than their egg-laying relatives, but overall teleosts do not deviate from the null 1:1 line ( $t = 0.957$ ; d.f. = 9;  $p = 0.388$ ) (figure 2).

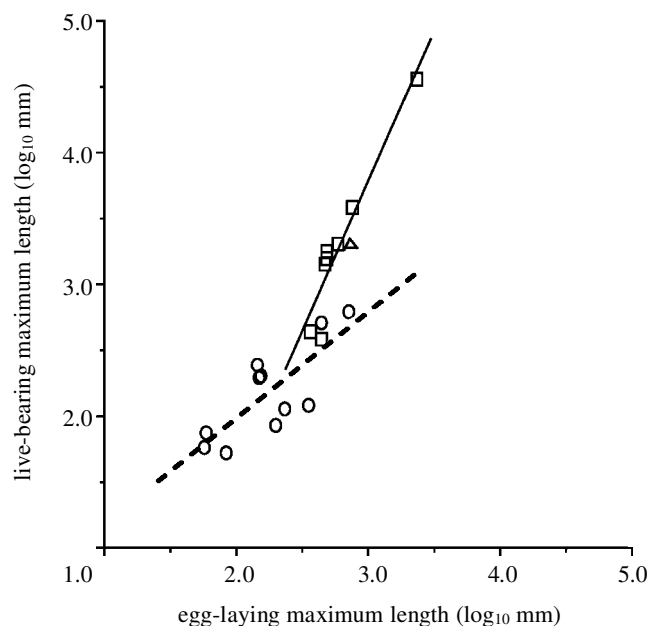


Figure 2. Phylogenetic comparison of maximum adult lengths between egg-laying and live-bearing sister clades ( $n = 20$ ). Each data point represents a paired comparison listed in Appendix A. Separate regression lines are shown for teleosts (circles, dashed line:  $y = 0.385 + 0.800x$ ;  $r^2 = 0.620$ ;  $t = 3.83$ ; d.f. = 10;  $p < 0.004$ ) and for elasmobranchs (squares, solid line:  $y = -3.061 + 2.284x$ ;  $r^2 = 0.897$ ;  $t = 7.22$ ; d.f. = 7;  $p < 0.001$ ). The triangle represents the coelacanth versus lungfish-tetrapod comparison.

#### 4. DISCUSSION

We found evidence for 12 transitions from egg laying to live bearing in bony fishes, bringing the total known transitions in fishes, including elasmobranchs (Dulvy & Reynolds 1997), to 21 to 22. This is considerably less than the estimates of 23 transitions for teleosts and at least 18 for elasmobranchs by Wourms (1994). Our literature review did not uncover any new taxa showing live bearing, though taxonomic revisions have shuffled them around somewhat (Appendix A). The reduced number of transitions is due to new phylogenetic revisions, suggesting that although fishes are second only to reptiles in terms of numbers of independent evolutionary transitions to live bearing (102 to 115 transitions) (Shine 1985; Blackburn 1999), their reproductive modes have been more conservative than previously thought. In addition, maximum parsimony analysis (using MACCLADE) showed no evidence for reversibility of live bearing (to egg laying) in teleost fishes. This supports similar evidence from the reptiles (Lee & Shine 1998), where previous evidence of reversals (De Fraipont *et al.* 1996) were based on weak empirical support (Lee & Shine 1998; Shine & Lee 1999). However, in elasmobranchs there is evidence for one to two reversals from live bearing to egg laying (Dulvy & Reynolds 1997). In the following we discuss our results in terms of the three main predictions for covariation among live bearing and other aspects of animal life histories.

##### (a) Body size

Fourteen out of the 20 comparisons supported the hypothesis that live bearers would be larger than egg lay-

ers. This pattern was dominated by the larger-bodied elasmobranchs, with larger live bearers in seven out of eight comparisons, compared with six out of 11 comparisons for teleosts. This result is opposite to a study by De Fraipont *et al.* (1996) who showed that live bearing in snakes and lizards was associated with a reduction in size. A decrease in size might relate to the reduction in fecundity in live-bearing reptiles (De Fraipont *et al.* 1996). However, we must treat their result with caution because of shortcomings in their phylogenetic comparisons and database (cf. Blackburn 1999; Shine & Lee 1999). Our results for elasmobranchs are consistent with the idea that larger size relaxes constraints on internal volume, which may be particularly acute in live-bearing species. Large size may also reduce predation pressures on adults (Miller 1979), which could be particularly important due to reduced mobility when carrying young (Fitch 1970; Thibault & Schultz 1978). However, one might expect teleosts to show the greatest response to this form of selection, since they are much smaller than elasmobranchs. The fact that increased size only occurs in elasmobranchs suggests that an anti-predation function may not have had a strong influence on the body size of live bearers. Instead, the difference may be due to the demands of greater maternal input by most live-bearing elasmobranchs than by teleosts.

##### (b) Offspring length and fecundity

Wourms & Lombardi (1992) hypothesized that live bearers would evolve larger offspring at the expense of fecundity. We found overall support for live bearers having larger offspring in all 13 comparisons, but live bearers are less fecund in approximately half (seven out of 11) of the comparisons. Therefore the hypothesis that live bearers are less fecund remains equivocal. Note, however, that this hypothesis may be weakened by the observed increase in body size among elasmobranch live bearers. Reduced reproductive effort was reported to be associated with live bearing in a comparison of commercial fish stocks (Gunderson 1997), though the comparison was limited to seven rockfish (Teleostei: Scorpaenidae), and one dogfish (Elasmobranchii: Squalidae), which were not compared to close relatives. Definitive conclusions about fecundity reductions are not possible until more data become available.

##### (c) Comparisons with other forms of care

Both internal and external parental care enhance individual offspring growth and survival (Clutton-Brock 1991). These contributions to the young may therefore evolve in response to similar selective forces (De Fraipont *et al.* 1996), such as spatially and temporally unpredictable environments (Wootton 1990) and cold climates (Shine 1983). Shine & Bull (1979) hypothesized that parental care is an intermediate step toward live bearing, but additional data to those provided by De Fraipont *et al.* (1996) are required before this hypothesis can be evaluated in squamate reptiles (Blackburn 1999; Shine & Lee 1999). Similarly, in fishes there are too few groups or data available to test this hypothesis, though we found that in four out of the 11 teleost comparisons the egg-laying sister taxa of live bearers provide external parental care (Appendix A). Parental care of external eggs has not been recorded in elasmobranchs (Breder & Rosen 1966;

Wourms 1977). Elasmobranch eggs may be at less risk because they have greater protection from a sclerotized case and are laid in or on the substrate (Wourms 1977).

These results provide support for hypotheses suggesting that live bearing is associated with large adult and offspring length, but there is little consistent evidence of reduced fecundity. Furthermore, correlations between body size, offspring length and fecundity are not consistent across teleosts and elasmobranchs. Studies that examine the duration and conditions of embryonic development, juvenile survival and biogeographical distribution should help to explain the costs and benefits that determine the evolution of live bearing across taxa.

This work was supported by Biotechnology and Biological Sciences Research Council studentships to N.B.G. and N.K.D. The authors are grateful to A. Berglund, W. Sutherland, M. Lee, S. Balshine and an anonymous referee for comments on the manuscript.

## REFERENCES

- Amoroso, E. C. 1968 The evolution of viviparity. *Proc. R. Soc. Med.* **61**, 1188–1200.
- Anderson, M. E. 1984 Zoarcidae, development and relationships. In *Ontogeny and systematics of fishes*, American Society of Ichthyologists and Herpetologists, special publication no. 1 (ed. H. G. Moser), pp. 579–582. Lawrence, KS: Allen Press.
- Balon, E. K. 1977 Early ontogeny of *Labeotropheus* Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. *Environ. Biol. Fish.* **2**, 147–176.
- Baylis, J. R. 1981 The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. *Environ. Biol. Fish.* **6**, 223–251.
- Blackburn, D. G. 1992 Convergent evolution of viviparity, matrotrophy, and specializations for fetal nutrition in reptiles and other vertebrates. *Am. Zool.* **32**, 313–321.
- Blackburn, D. G. 1999 Are viviparity and egg-guarding evolutionarily labile in squamates? *Herpetologica* **55**, 556–573.
- Blaxter, J. H. S. 1992 The effect of temperature on larval fishes. *Neth. J. Zool.* **42**, 336–357.
- Boehlert, G. W., Kusakari, M. & Yamada, J. 1991 Oxygen consumption of gestating female *Sebastes schlegelii*: estimating the reproductive costs of live bearing. *Environ. Biol. Fish.* **30**, 81–89.
- Breder, C. M. & Rosen, D. E. 1966 *Modes of reproduction in fishes*. New York: Natural History Press.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton University Press.
- Cohen, D. M. & Nielsen, J. G. 1978 *Guide to the identification of genera of the fish order Ophidiiformes with a tentative classification of the order*, NOAA technical report, NMFS circular 417. Seattle, WA: US Department of Commerce.
- Collette, B. B. 1995 *Tondanichthys kottelati*, a new genus and species of freshwater halfbeak (Teleostei, Hemiramphidae) from Sulawesi. *Ichth. Explor. Freshwat.* **6**, 171–174.
- Compagno, L. J. V. 1988 *Sharks of the order Carcharhiniformes*. Princeton University Press.
- De Fraipont, M., Clobert, J. & Barbault, R. 1996 The evolution of oviparity with egg guarding and viviparity in lizards and snakes: a phylogenetic analysis. *Evolution* **50**, 391–400.
- Dingerkus, G. 1983 A revision of the Orectolobiform shark family Hemiscyllidae (Chondrichthyes, Selachii). *Bull. Am. Mus. Nat. Hist.* **176**, 1–94.
- Dingerkus, G. 1986 Interrelationships of Orectolobiform sharks (Chondrichthyes, Selachii). In *Indo-Pacific fish biology: Proc. 2nd Int. Conf. Indo-Pacific Fishes* (ed. T. Uyeno, R. Arai, T. Taniuchi & K. Matsuura), pp. 227–245. Tokyo: Ichthyological Society of Japan.
- Duarte, C. M. & Alcaraz, M. 1989 To produce many small or few large eggs: a size-independent reproductive tactic of fish. *Oecologia* **80**, 401–404.
- Dulvy, N. K. & Reynolds, J. D. 1997 Evolutionary transitions among egg-laying, live-bearing and maternal inputs in sharks and rays. *Proc. R. Soc., Lond. B* **264**, 1309–1315. (DOI 10.1098/rspb.1997.0181.)
- Elgar, M. A. 1990 Evolutionary compromise between a few large and many small eggs, comparative evidence in teleost fish. *Oikos* **59**, 283–287.
- Eschmeyer, W. N. (ed.) 1998 *Catalog of fishes*. San Francisco, CA: California Academy of Sciences.
- Fitch, H. S. 1970 Reproductive cycles in lizards and snakes. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* **52**, 1–247.
- Froese, R. & Binohlan, C. 2000 Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *J. Fish Biol.* **56**, 758–773.
- Fry, F. E. J. 1971 The effect of environmental factors on the physiology of fish. In *Fish physiology* (ed. W. S. Hoar & D. J. Randall), pp. 1–98. London: Academic Press.
- Grudzien, T. A., White, M. M. & Turner, B. J. 1992 Biochemical systematics of the viviparous fish family Goodeidae. *J. Fish Biol.* **40**, 801–814.
- Gunderson, D. R. 1997 Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Can. J. Fish. Aqua. Sci.* **54**, 990–998.
- Ishida, M. 1994 Phylogeny of the suborder Scorpaenoidei (Pisces, Scorpaeniformes). *Nansei Reg. Fish. Res. Lab. Bull.* **27**, 112.
- Lee, M. S. Y. & Shine, R. 1998 Reptilian viviparity and Dollo's law. *Evolution* **52**, 1441–1450.
- McEachran, J. D., Dunn, K. A. & Miyake, T. 1996 Interrelationships of the Batoid fishes (Chondrichthyes, Batoidea). In *Interrelationships of fishes* (ed. M. L. J. Stiassny, L. R. Parenti & G. D. Johnson), pp. 63–84. London: Academic Press.
- Maddison, W. P. 2000 Testing character correlation using pairwise comparisons on a phylogeny. *J. Theor. Biol.* **202**, 195–204.
- Maddison, W. P. & Maddison, D. R. 1992 *MACCLADE, analysis of phylogeny and character evolution*, v. 3.07. Sunderland, MA: Sinauer Associates.
- Meyer, A. & Lydeard, C. 1993 The evolution of copulatory organs, internal fertilization, placenta and viviparity in killifishes (Cyprinodontiformes) inferred from a DNA phylogeny of the Tyrosine Kinase gene *X-src*. *Proc. R. Soc. Lond. B* **254**, 153–162.
- Miller, P. J. 1979 Adaptiveness and implications of small size in teleosts. *Symp. Zool. Soc. Lond.* **44**, 263–306.
- Parenti, L. R. 1981 A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). *Bull. Am. Mus. Nat. Hist.* **168**, 335–557.
- Qualls, C. P. & Shine, R. 1995 Maternal body-volume as a constraint on reproductive output in lizards: evidence from the evolution of viviparity. *Oecologia* **103**, 73–78.
- Qualls, C. P. & Shine, R. 1998 *Lerista bougainvillii*, a case study for the evolution of viviparity in reptiles. *J. Evol. Biol.* **11**, 63–78.
- Sergeev, A. M. 1940 Researches in the viviparity of reptiles. *Moscow Soc. Naturalists* (Jubilee Issue), 1–34.
- Shine, R. 1978 Propagule size and parental care: the 'safe harbor' hypothesis. *J. Theor. Biol.* **75**, 417–424.
- Shine, R. 1983 The evolution of viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. *Oecologia* **57**, 397–405.

Shine, R. 1985 The evolution of viviparity in reptiles: an ecological analysis. In *Biology of the Reptilia*, vol. 15 (ed. C. Gans & F. Billet). New York: Wiley.

Shine, R. 1989 Ecological influences on the evolution of vertebrate viviparity. In *Complex organismal functions, integration and evolution in vertebrates* (ed. D. B. Wake & G. Roth), pp. 263–278. New York: Wiley.

Shine, R. 1994 Sexual size dimorphism in snakes revisited. *Copeia* **1994**, 326–346.

Shine, R. 1995 A new hypothesis for the evolution of viviparity in reptiles. *Am. Nat.* **145**, 809–823.

Shine, R. & Bull, J. J. 1979 The evolution of live-bearing in lizards and snakes. *Am. Nat.* **113**, 905–923.

Shine, R. & Lee, M. S. Y. 1999 A reanalysis of the evolution of viviparity and egg-guarding in squamate reptiles. *Herpetologica* **55**, 538–549.

Slobodyanyuk, S. J., Kirilchik, S. V., Pavlova, M. E., Belikov, S. I. & Novitsky, A. L. 1995 The evolutionary relationships of two families of cottoid fishes of Lake Baikal (East Siberia) as suggested by analysis of mitochondrial DNA. *J. Mol. Evol.* **40**, 392–399.

Stepien, C. A., Dixon, M. T. & Hillis, D. M. 1993 Evolutionary relationships of the blennioid fish families Clinidae, Labrisomoidae and Chaenopsidae: congruence between DNA sequence and allozyme data. *Bull. Mar. Sci.* **52**, 496–515.

Streelman, J. T. & Karl, S. A. 1997 Reconstructing labroid evolution with single-copy nuclear DNA. *Proc. R. Soc. Lond. B* **264**, 1011–1020. (DOI 10.1098/rspb.1997.0140.)

Thibault, R. E. & Schultz, R. J. 1978 Reproductive adaptations among viviparous fishes (Cyprinodontiformes, Poeciliidae). *Evolution* **32**, 320–333.

Tohyama, Y., Ichimiya, T., Kasama-Yoshida, H., Cao, Y., Hasegawa, M., Kojima, H., Tamai, Y. & Kurihara, T. 2000 Phylogenetic relation of lungfish indicated by the amino acid sequence of myelin DM20. *Mol. Brain Res.* **80**, 256–259.

Visman, V., Pesant, S., Dion, J., Shipley, B. & Peters, R. H. 1996 Joint effects of maternal and offspring sizes on clutch mass and fecundity in plants and animals. *Ecoscience* **3**, 173–182.

Wootton, R. J. 1990 *Ecology of teleost fishes*. London: Chapman & Hall.

Wourms, J. P. 1977 Reproduction and development in chondrichthyan fishes. *Am. Zool.* **17**, 379–410.

Wourms, J. P. 1981 Viviparity, the maternal–fetal relationship in fishes. *Dev. Biol. Fish.* **21**, 473–515.

Wourms, J. P. 1993 The reproduction and development of sharks, skates, rays and ratfishes: introduction, history, overview, and future projects. *Environ. Biol. Fish.* **38**, 7–21.

Wourms, J. P. 1994 The challenges of piscine viviparity. *Israel J. Zool.* **40**, 551–568.

Wourms, J. P. & Cohen, D. M. 1975 Trophotaeniae, embryonic adaptations, in the viviparous ophidioid fish, *Oligopus longhursti*: a study of museum specimens. *J. Morphol.* **147**, 385–402.

Wourms, J. P. & Lombardi, J. 1992 Reflections on the evolution of piscine viviparity. *Am. Zool.* **32**, 276–293.

Zar, J. H. 1996 *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice-Hall.

APPENDIX A

Table A1. Summary of live-bearing and egg-laying phylogenetic comparisons with life-history information for Teleostei (bony fishes), Elasmobranchii (sharks and rays), and Sarcopterygii (coelacanth, lungfish and tetrapods). (Nested means of life-history characters are shown for each half of the live-bearing–egg-laying comparison. Abbreviation: exc., excluding taxa.)

sister comparison	reproductive mode	life-history character			phylogenetic references
		maximum length (mm)	offspring length (mm)	mean fecundity	
Teleostei					
1 <sup>a</sup> Hemiramphidae					
<i>Dermogenys</i>	live	85.0	17.5	13.6	Collette (1995)
<i>Hemiramphodon</i>	live				
<i>Normorhampus</i>	live				
<i>Todamichthys</i>	live				
<i>Zenarchopterus</i>	egg	193.3	—	97.6	
2 <sup>a</sup> Anablepidae					
Anablepinae	live	200	47.3	19.9	Parenti (1981) and Meyer & Lydeard (1993)
Oxyzygonectinae	egg	150	—	—	
3 <sup>a</sup> Goodeidae					
Goodeinae	live	76.1	13.1	19.9	Parenti (1981) and Grudzien <i>et al.</i> (1992)
Empetrichthyinae	egg	58.3	—	13.5	
4 <sup>a</sup> Poeciliidae					
Poecilinae	live	58.9	7.4	26.8	Parenti (1981) and Meyer & Lydeard (1993)
Aplocheilichthyinae	egg	56.3	—	—	
Fluviphylacinae	egg				

Continued

Table A1. *Continued*

	sister comparison	reproductive mode	life-history character			phylogenetic references
			maximum length (mm)	offspring length (mm)	mean fecundity	
5	Ophidiiformes					
	Bythitoidei	live	122.9	10.0	1334.8	Cohen & Nielsen (1978)
	Ophidioidei	egg	346.1	—	—	
6	Clinidae					
	Clinini & Ophiclinini	live	112.1	10.7	106.9	Stepien <i>et al.</i> (1993)
	Myxodini	egg	231.7	9.0	—	
7	Labrisomidae					
	<i>Starksia</i>	live	52.8	5.0	64.5	Stepien <i>et al.</i> (1993)
	<i>Xenomedeia</i>	live				
	Chaenopsidae	egg <sup>b</sup>	82.0	—	—	
	Labrisomidae	egg				
8	Embiotocidae	live	244.9	47.3	22.5	Streelman & Karl (1997)
	Pomacentridae	egg <sup>b</sup>	142.2	12.6	—	
9	Zoarcidae					
	<i>Zoarces</i> sp.	live	610	41.5	50	M. E. Anderson (unpublished data) and Anderson (1984)
	<i>Zoarces americanus</i>	egg <sup>b</sup>	711	33.0	2700	
10	Sebastidae					
	Sebastinae	live	515.9	4.7	20 4414	Ishida (1994)
	Sebastolobinae	egg	440.0	—	—	
11 <sup>a</sup>	Comephoridae	live	195.0	9.4	1900.4	Slobodyanyuk <i>et al.</i> (1995)
	Cottidae					
	<i>Paracottus</i>	egg <sup>b</sup>	144.7	5.3	4073.5	
Elasmobranchii						
12	Scyliorhinidae					
	<i>Galeus arae</i>	live	380.0	120.0	—	Compagno (1988)
	<i>Galeus polli</i>	live				
	<i>Galeus spp.</i>	egg	482.9	101.5	7.5	
13	<i>Halaehurus</i>	live	461.2	149.6	17	Compagno (1988)
	<i>Haplobepharus</i>	egg	392.5	104.9	2	
	<i>Holohalaehurus</i>	egg				
14	Proscylliidae					
	<i>Eridacnis</i>	live	277.5	123.3	1.8	Compagno (1988)
	<i>Ctenacis</i>	egg	—	—	2.0	
	<i>Proscyllium</i>	egg				
15	Pseudotriakidae	live	2026.0	797.5	2.0	Compagno (1988)
	Proscylliidae					
	<i>Ctenacis</i>	egg	516.7	116.3	2.7	
	<i>Proscyllium</i>	egg				
	Scyliorhinidae	egg				
	exc. <i>Eridacnis</i>					
	<i>Galeus arae</i>					
	<i>Galeus polli</i>					
	<i>Halaehurus</i>					

*Continued*



Table A1. *Continued*

sister comparison		reproductive mode	life-history character			phylogenetic references			
			maximum length (mm)	offspring length (mm)	mean fecundity				
16	Leptocharidae	live	2330.0	280.0	4.0	Compagno (1988)			
	Triakidae	live							
	Hemigaleidae	live							
	Carcharhinidae	live							
	Sphrynidae	live							
	Proscylliidae		516.7	116.3	2.7				
	<i>Ctenacis</i>	egg							
	<i>Proscyllium</i>	egg							
	Scyliorhinidae	egg							
	exc. <i>Eridacnis</i>								
	<i>Galeus arae</i>								
<i>Galeus polli</i>									
<i>Halaehurus</i>									
17	Orectolobiformes		36000.0	570	142	Dingerkus (1983, 1986)			
	Rhincodontidae	live							
	Stegastomatidae	egg							
18	Ginglymostomatidae	live	10635	418.3	56.9	Dingerkus (1983, 1986)			
	Rhincodontidae	egg							
	Hemiscylliidae	egg							
19	Brachaeluridae	live	2357.5	194.2	11.8	Dingerkus (1983, 1986)			
	Orectolobidae	live							
	Parascylliidae	egg							
20	Rajiformes		2433.6	429.1	5.1	McEachran <i>et al.</i> (1996)			
	Myliobatoidea	live							
	Rajidae	egg							
Sarcopterygii 21	Coelacanthiformes	live	1990	320	10.5	Tohyama <i>et al.</i> (2000)			
	Latimeriidae								
	Dipnoi <sup>c</sup>	egg <sup>c</sup>					771	7	<i>ca.</i> 2857
	Tetrapods <sup>c</sup>	egg <sup>c</sup>							

<sup>a</sup> Freshwater taxa.<sup>b</sup> Groups providing parental care.<sup>c</sup> Estimates of mean fecundity were available for tetrapods but not for Dipnoi due to lack of data.