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Evolutionary transitions in parental care and live bearing in vertebrates

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We provide the first review of phylogenetic transitions in parental care and live bearing for a wide variety of vertebrates. This includes new analyses of both numbers of transitions and transition probabilities. These reveal numerous transitions by shorebirds and anurans toward uniparental care by either sex. Whereas most or all of the shorebird transitions were from biparental care, nearly all of the anuran transitions have been from no care, reflecting the prevalence of each form of care in basal lineages in each group. Teleost (bony) fishes are similar to anurans in displaying numerous transitions toward uniparental contributions by each sex. Whereas cichlid fishes have often evolved from biparental care to female care, other teleosts have usually switched from no care to male care. Taxa that have evolved exclusive male care without courtship-role reversal are characterized by male territoriality and low costs of care per brood. Males may therefore benefit from care through female preference of parental ability in these species. Primates show a high frequency of transitions from female care to biparental care, reflecting the prevalence of female care in basal lineages. In the numerous taxa that display live bearing by females, including teleosts, elasmobranchs, squamate reptiles and invertebrates, we find that live bearing has always evolved from a lack of care. Although the transition counts and probabilities will undoubtedly be refined as phylogenetic information and methodologies improve, the overall biases in these taxa should help to place adaptive hypotheses for the evolution of care into a stronger setting for understanding directions of change.

Keywords: comparative study; Charadriiformes; amphibian; reptile; mammal; invertebrate

1. INTRODUCTION

Parental care and live bearing are fundamental aspects of the life histories of many animal taxa, and include an enormous diversity of forms of input to the young (Clutton-Brock 1991). Theory predicts that differences in parental care patterns among species arise from interspecific differences in the benefits for offspring survival versus parental costs, such as reduced parental survival, fecundity and mating opportunities (e.g. Clutton-Brock 1991; Székely *et al.* 1996; Sargent 1997).

Although within-species studies have been important in revealing costs and benefits of care, these studies do not enable us to trace the evolutionary pathways that have led to contemporary diversity. Furthermore, there are usually limits in the extent to which parental care can be manipulated in experimental tests of causes and consequences. For example, it is rarely possible to coerce males to provide care in species in which females normally have sole responsibility for this task.

Phylogenetic studies provide a complementary means of understanding the evolution of parental care because they allow the reconstruction of historical routes to contemporary patterns. Indeed, different hypotheses concerning the evolution of parental care often make different predictions about the directions of change, and these can be tested by tracing changes in care along an evolutionary tree. Furthermore, by taking advantage of large differences among taxa, phylogenies enable tests of hypotheses for benefits and costs of care that are often impossible to test experimentally because of limited flexibility within species. Our ability to make inferences from phylogenetic information has been aided by recent advances in the use of molecular data to generate phylogenetic trees, as well as improvements in the ease with which databases can be compiled through computer searches.

In this paper, we examine evolutionary transitions in parental care and live bearing in a variety of vertebrate taxa. The focus on vertebrates stems from our own taxon biases, though we also attempt some brief comparisons with invertebrates. In fact, vertebrates have provided some of the best documented tests of general hypotheses regarding phylogenetic transitions. We are concerned with differences between the sexes in parental contributions, including live bearing, with specific emphasis on four character states: no care, male care, female care, and biparental care. We include any behaviour that involves remaining with the young and looking after them, but not choice of sites to deposit the young or preparation of such sites. We have included live bearing as a form of female 'care', though strictly this should be considered a form of 'expenditure', as it is more concerned with energetic input to the offspring than behaviour *per se* (Clutton-Brock 1991). However, this distinction does not prevent us from testing general scenarios that have been proposed regarding sex differences in parental contributions to the young.

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2. FROM THEORIES TO TREES

Hypotheses about the evolution of parental care are often taxon specific: all birds have parental care, but one can debate whether or not their ancestors provided care, and whether biparental care gave rise to male care or to female care (e.g. Burley & Johnson 2002; Tullberg *et al.* 2002). In principle, it should be straightforward to measure changes in the frequency of different forms of parental care using ancestral state reconstruction to trace changes along a phylogeny (Maddison & Maddison 1992). A problem with using a simple count of numbers of state transitions is that counts ignore the frequencies with which different traits occur (Harvey & Pagel 1991). A very common trait, for example, is more likely to be observed to change to another state than will a rare trait simply because it is abundant. More generally the change in state of discrete characters may be measured as a transition rate, i.e. the probability of a trait evolving into another state, or alternatively of remaining the same (Harvey & Pagel 1991; Pagel 1994). Only one relevant phylogeny (primates: Purvis 1995) presented branch lengths. However, even when branch-length information is not available, probabilities based on the assumption that all branch lengths are the same should improve on simple counts (Harvey & Pagel 1991). Rather than calculating rates of transitions between character states per unit time, we calculated the rate of transition as the proportion of nodes allocated a particular character state that changed to the other state, or else remained constant (e.g. Grafen & Ridley 1996). For instance, suppose there are two alternative states of a single trait. Then if a total of X nodes were observed at some time or other to be in state 0, and of these X_{00} remained in state 0, while X_{01} changed to the other state 1, then the probability of stasis would be $P_{00} = X_{00}/X$, and the probability of changing to state 1 would be $P_{01} = X_{01}/X$. In general, for n character states this yields an $n \times n$ matrix of observed transition probabilities (of which several entries will be zero, representing no observed transitions). In order to generate confidence intervals for the probabilities, we used the observed probabilities to simulate character evolution on the given phylogeny. For each matrix and phylogeny, we generated confidence intervals from 10 000 replicate simulations. Both counts and transition probabilities are only approximate estimates of the true amount of evolutionary change and will be influenced by extinction rates, the intensity of taxon sampling and the availability of branch-length information.

In each of the analyses presented below, we give counts of transitions between the sex of care givers as well as parity (egg laying versus live bearing). For the data from anurans, elasmobranchs, cichlid fishes, shorebirds and primates, for which phylogenies were available, we calculated probabilities of transition between states as well as counting the number of transitions.

Most reasoning about provision of care is game theoretical, because the responses of one sex will depend on the behaviour of the other as well as parent–offspring conflicts (reviewed by Parker *et al.* (2002)). Although much of the theory discussed below has not yet been cast in formal game-theory models, the game-theoretical reasoning still implicitly underlies the discussions.

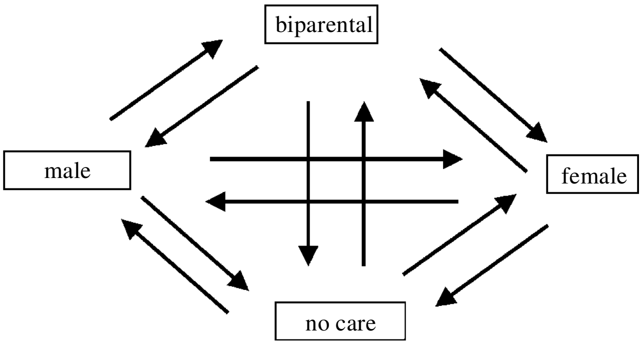

Figure 1. Potential transitions among parental care states, allowing for either sex to remain with or abandon the young.

There are a huge number of potential transitions that could occur within a clade between male care, female care, biparental care and no care, especially if one allows for reversals, cyclical dynamics and switches from any state to any other one. In fact, most hypotheses assume that evolution moves one step at a time in either direction between the pairs of character states shown in figure 1. Thus, either males or females may be selected to remain with the young or to desert the brood. Although we focus primarily on patterns of such transitions, we also consider briefly the phylogenetic evidence that bears on processes that may have led to these changes, including selection due to the environment and costs to parents through trade-offs with other aspects of life histories and sexual selection. We review the major groups of vertebrates in approximate taxonomic order.

3. VERTEBRATE STUDIES

(a) *Fishes*

(i) *Teleosts overall*

Teleost (bony) fishes display all four of the potential care states shown in figure 1 (e.g. Blumer 1979). They have inspired a great deal of early thinking about the evolution of parental care (e.g. Barlow 1974; Williams 1975; Baylis 1981; Gross & Sargent 1985; Sargent & Gross 1993).

It has been proposed that a lack of care, which is most prevalent in fishes, was the ancestral state, from which male care (the next most prevalent state) was the most common next step. Transitions are thought to have continued in a clockwise direction around the states shown in figure 1 (Gittleman 1981; Gross & Sargent 1985). The first step toward male care may have been facilitated by male territoriality, which could predispose males to guarding and caring for one or more clutches at the same time (Williams 1975). It has been suggested that males can do this without unduly compromising mating opportunities because the embryos and larvae of fishes do not need to have heat or food given to them, unlike the case for birds and mammals. Males can therefore care for the broods of more than one female at a time. If females were to provide care, their future fecundity costs due to energetic expense might be less compensated by enhanced present reproductive success than would be the case for males (Gross & Sargent 1985). High confidence of paternity may also facilitate the evolution of male care under some circumstances, though this issue is far from straightforward (reviewed by Sheldon (2002)). The care–sexual-selection trade-off in fishes is further weakened if females are attracted to males that are already caring for eggs. A recent review documented this for 13 species of fishes (Reynolds & Jones 1999). Not all of these studies were conclusive, and there is probably a publication bias towards positive results. However, this evidence suggests that in fishes, male care and sexual selection may reinforce one another, rather than acting in strong opposition, as in endothermic vertebrates.

Females may have been selected to join the males if egg sizes increased under male care, which would lead to longer development times, and hence selection for more parental input (Gross & Sargent 1985). However, cause and effect could be reversed if care selects for larger eggs (Nussbaum & Schultz 1989). Presumably, females could also be selected to join males if the environment changed, and if the needs of the young for the services of an extra parent outweighed the costs to that parent.

From biparental care, changes in sexual selection or the environment could enter the picture again, this time causing males to desert to maximize mating opportunities. Here, we are on familiar ground with standard arguments for trade-offs between sexual selection and parental care (reviewed by Andersson (1994) and Reynolds (1996)). In support of this, studies have shown experimentally that in biparental species of fishes, males are prone to desert females earlier when extra-mating opportunities are provided (Keenleyside 1983; Balshine-Earn & Earn 1998). Note also, however, that experiments have shown that female biparental cichlids may desert males when they are given extra-mating opportunities (Balshine-Earn & Earn 1998). In fishes, female care may also become unstable, leading back to no care (Gittleman 1981; Gross & Sargent 1985). The theory for this proposed instability has not been developed in detail, but one might imagine a change in the environment such that the costs of care become too high, or the benefits become too small. For example, predation rates on eggs and larvae could become reduced. Then, female care could give rise to no care, and teleost fishes could therefore exhibit cyclical patterns of transitions.

The first phylogenetic test of these ideas for teleost fishes was performed by Gittleman (1981). This study, which was well ahead of its time, found some phylogenetic support for the proposed transitions, based on an analysis of a very limited number of families and genera (21). Transitions among care states were inferred by counting the number of teleost fish families and genera that contained more than one care state. The directions of transition were then inferred from outgroup analyses. Gross & Sargent (1985) updated the numbers of families containing one or more parental care state. We present the counts of families providing a single form of care in table 1. This confirms the domination of male care among the 21% of teleost families in which care is provided. Gittleman (1981) emphasized that the transitions that he inferred are preliminary. These counts are also shown in table 1. Note that there is no evidence regarding the proposed transition between female care and no care.

This study was limited to a small number of comparisons, and no study has taken advantage of the modern methods that are available to use formal phylogenetic procedures for reconstructing ancestral character states in a diverse array of fishes. This is a daunting task, given the fragmentary nature of teleost phylogenies, and the large number of species involved. We have begun these analyses, and our own preliminary results suggest that the proposed transition from no care to male care probably does dominate, though we are less certain about the direction of transitions between no care and female care.

(ii) *Teleosts: cichlids*

Members of the family Cichlidae comprise more than 1300 described species in about 195 genera. They are widespread in Africa and Central and South America. All species provide parental care. A recent review found evidence that 73 genera provide biparental care, and 108 genera have female care (Goodwin *et al.* 1998). Exclusive male care has been documented unequivocally for one species (*Sarotherodon melanotheron*). The diversity of forms of parental care is unusually large for a single family of animals. In accordance with the expectation for teleost fishes in general (reviewed above), it had been proposed that the main direction of transition has been from biparental to female-only care (Keenleyside 1991).

A composite phylogeny was compiled for the family based on 12 published studies, and care was optimized onto it using parsimony (Goodwin *et al.* 1998). No prior assumptions were made about probabilities of directions of transitions, i.e. the character states were unordered. The analyses supported the predicted bias in transitions, with 21–30 changes from biparental care to uniparental female care, and 0–10 transitions in the other direction. The ranges of transitions depend on how one resolves equivocal ancestral branches. As with all phylogenetic studies, the relationships among taxa are themselves hypotheses, and the inferences from them depend on the trees being unbiased with respect to the question. Fortunately, when the analyses were done using eight alternative variants on the composite phylogeny, all analyses pointed to the same bias in transitions from biparental to female care. This interpretation is further reinforced by new analyses of transition rates; we calculate the rate of transition from biparental care to be 0.12 (95% CI 0.06–0.40)—that is, 12% of biparental lineages are inferred to have switched to female care.

S. Balshine, N. B. Goodwin and J. D. Reynolds (unpublished data) have attempted to explain the process behind the pattern of evolutionary reductions in care provided by male cichlids. There is evidence that species in which care is provided solely by the female occur in habitats that have significantly fewer species of fishes that could prey on offspring. This suggests that either desertion by males has been facilitated by benign environmental conditions, or that there has been a habitat shift by such taxa after male desertion. Directional phylogenetic tests are needed to distinguish between these possibilities (see Harvey & Pagel 1991; Pagel 1994).

(iii) *Elasmobranchs*

Sharks and rays (Elasmobranchii) comprise approximately 815 described species. They do not provide care in the sense of behavioural contributions to the young after oviposition. However, many species are live bearers, with

Table 1. Incidence and evolutionary transitions in parental care in vertebrates.

(Live bearing is excluded (see table 2). Data for percentages of taxa showing forms of care pertain to taxonomic levels indicated for each column heading. Transition counts can be understood with the following example for teleost fishes: 5/0 for the category 'none to/from male' denotes five transitions from no care to male care and zero transitions from male care to no care. Percentages for teleosts are based on numbers of families and genera that show exclusively one form of care, and transition counts are extremely preliminary, based on a limited survey and only showing transitions for which there was reasonable support. Cichlid fishes are a family of teleosts. Anuran percentages add up to more than 100% because 28 genera exhibit more than one form of care. Birds were aggregated among taxa, and the minimum estimates of transitions are very preliminary. Shorebird percentage data are based on 96 of approximately 203 species. Their data refer to the predominant care giver and are not directly comparable with scores of other taxa (but see figure 4*a*, which includes gulls and allies.)

	teleost fishes 422 families	cichlid fishes 182 genera	anurans 315 genera	mammals 1117 genera	primates 203 species	squamate reptiles 938 genera	crocodilians 21 species	birds 9600 species	shorebirds 203 species
% no care	79	0	92	0	0	97	0	0	0
% male-only care	10	< 1	9	0	0	0	0	< 1	44
% biparental care	3	40	1	9	32	0	38	90–95	44
% female-only care	1	60	9	91	68	3	62	5–10	13
none to/from male	5/0	—	21–22/0–1	—	—	—	—	—	—
none to/from biparental	0/0	—	2–3/0	—	—	—	—	—	—
none to/from female	0/1	—	18–20/0	—	—	?	1/0	—	—
male to/from biparental	1/0	0/1	2/0	—	—	—	—	2/2	5–11/2–6
male to/from female	0/0	0/0	1–2/0–1	—	—	—	—	1/0	6–8/0
biparental to/from female	?	21–30/0–10	1–2/0–1	?	3–8/17–23	—	0/2–3	7/0	0–3/0–3
references[a]	1, 2	3	4, 5	6	7	8	9, 10, 11	12, 13, 14	15

[a] References: 1, Gross & Sargent 1985; 2, Gittleman 1981; 3, Goodwin *et al.* 1998; 4, new analyses based partly on Beck (1998); 5, Clough & Summers 2000; 6, Kleiman & Malcolm 1981; 7, new analyses based on Kleiman & Malcolm (1981) and Purvis (1995); 8, De Fraipont *et al.* 1996; 9, Greer 1971; 10, Densmore & White 1991; 11, Aggarwal *et al.* 1994; 12, Lack 1968; 13, Vehrencamp 2000; 14, Oring 1982; 15, Székely & Reynolds 1995.

females providing a range of services. These include simple retention of embryo cases inside their oviducts until the young hatch and leave immediately, or provision of additional nutritional contributions, such as fats and proteins, that may be absorbed by embryos or supplied via direct placental blood-vessel links (Wourms 1981; Blackburn 1992; Dulvy & Reynolds 1997). Extrapolations from a literature survey indicated that *ca.* 40% of extant species are egg layers (Dulvy & Reynolds 1997) (table 2). In ascending order of additional maternal contributions by live bearers, *ca.* 18% of species have live bearing with no additional energetic input by the female other than her initial contribution of yolk (leicithotrophy), 31% supplement their yolk with uterine analogues of milk (forms of matrotrophy), and 9% of species have placental structures (other forms of matrotrophy). This diversity of reproductive modes is unusual, rivalled only by reptiles (Shine 1985*a*) and teleost fishes (Goodwin *et al.* 2002).

Elasmobranchs can be used to distinguish between two hypotheses about the directions of transitions between no care (egg laying) and female input (live bearing). The ancestral state in elasmobranchs has been proposed to be either the former (Wourms 1977) or the latter (Lund 1980). Dulvy & Reynolds (1997) tested these ideas by mapping reproductive modes onto a composite phylogeny of sharks and rays. The results suggested that egg laying was ancestral in elasmobranchs, and that live bearing has evolved 9–10 times (figure 2*a*). In terms of the probability of state change, our new analyses similarly indicate that the probability of an egg-laying species evolving live bearing is comparatively high, as *ca.* 14% of egg-laying nodes are observed to change to live bearing (figure 2*b*). Interestingly, there was evidence for two reversals to egg laying: once in temperate skates (Rajidae) and once in the branch leading to the zebra shark (*Stegostoma fasciata*). When live bearing was broken down into two forms—with and without post-fertilization maternal input—evolutionary transitions proved to have been highly labile, with many reversals from 'advanced' live bearing with maternal input to a simpler form restricted to yolk investment (figure 2*c*). In this case, the probability of transition from the intermediate form to the advanced form is approximately the same as the probability of the reverse transition (figure 2*d*). Also, the intermediate form is often omitted (or extinct), with evolution directly from egg laying to live bearing with maternal input (figure 2*b*). Indeed, the probability of the transition from egg laying to live bearing with maternal input is not much lower than the probability of changing to this state from the intermediate yolk-only form of live bearing.

(b) *Amphibians*

Most amphibians (frogs, toads, salamanders and caecilians) do not provide parental care (table 1). However, in those who do, they share with teleost fishes the distinction of being the only group of vertebrates that exhibits all four forms of parental care (no care, male care, female care and biparental care). Parental contributions are extremely diverse, including egg guarding, transport of tadpoles orally or on the adults' bodies, or live bearing.

We optimized parental care onto a composite phylogeny of anurans (frogs and toads) to estimate transitions using unordered character states and parsimony (figure 3, table 1). The data came from Beck (1998 and personal communication), as well as Clough & Summers (2000 and K. Summers, personal communication). Roughly half of the transitions were from no care to male care, and half were from no care to female care (figure 3*a*, table 1). There were few reversals. Interestingly, poison frogs (Dendrobatidae) appear to have followed the same sequence that has been proposed for teleost fishes, with one early transition from no care to male care, then two transitions from male to biparental, and one from biparental to female care (Clough & Summers 2000; K. Summers, personal communication). What is not evident from figure 3*a* is that, although there have been four to six transitions to biparental care from the other forms, biparental care appears to be somewhat labile, as 25% (two out of eight) of taxa inferred to be biparental reverted to female uniparental care (figure 3*b*). Otherwise it is clear from these transition probabilities that parental care has been extremely labile in this group, with the probabilities of transition being similar among the various character states (in the range 0.01–0.06) for most transitions.

In another group of amphibians—the caecilians—egg laying appears to be ancestral, and there is evidence for at least one transition to live bearing, which occurs in three families (Wilkinson & Nussbaum 1998). It is not clear how many times live bearing has evolved independently in caecilians, nor whether there have been reversals to egg laying.

(c) *Mammals*

(i) *Overall patterns*

Females provide parental care in all mammal species, and all are live bearers except for the two families of monotremes, represented by the platypus (Ornithorhynchidae) and the spiny anteater (Tachyglossidae), which lay a single egg. Zeller (1999) has shown that marsupial ancestors were egg layers, therefore suggesting that live bearing has evolved twice, once in the lineage that gave rise to the marsupials and once in the eutherian lineage (table 2). Marsupial reproduction involves a short period of gestation and lactation during which females can manipulate offspring growth by delayed implantation or embryonic diapause in response to unfavourable environmental conditions (Low 1978). By contrast, eutherians have long gestation periods and produce large offspring that are weaned relatively quickly (Clutton-Brock 1991).

Males aid females in providing care in *ca.* 9% of mammalian genera (Kleiman & Malcolm 1981), including taxa such as carnivores, primates and rodents (Woodroffe & Vincent 1994) (table 1). Male care may include feeding, guarding, grooming, carrying and teaching, and in some rodents males huddle with the young to keep them warm (Kleiman & Malcolm 1981; Dewsbury 1985; Woodroffe & Vincent 1994).

(ii) *Primates*

We investigated the evolution of biparental care in primates using the total evidence composite phylogeny of Purvis (1995) and data summarized by Kleiman & Malcolm (1981) and Woodroffe & Vincent (1994). When we optimize care over the phylogeny, we find that despite the low prevalence of biparental care, it has evolved from female care on numerous occasions (table 1). It has also been lost at least three times. In fact, the probability of

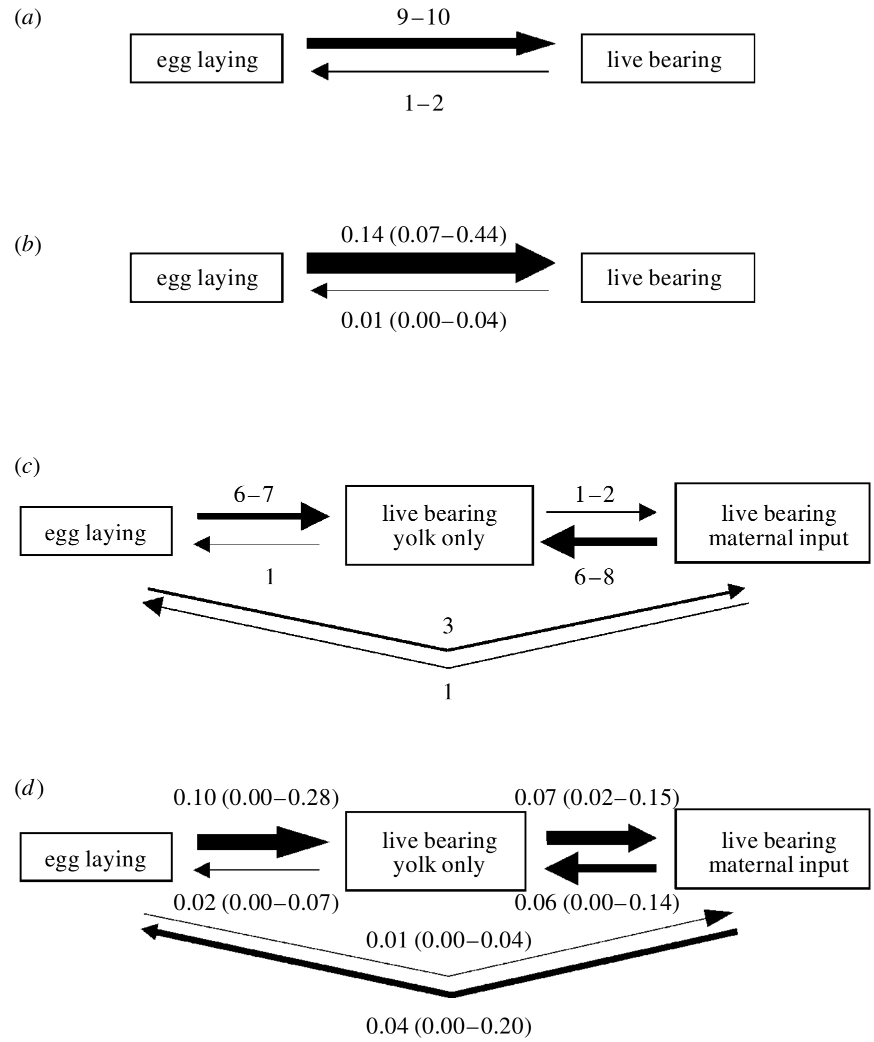

Figure 2. Evolutionary transitions between egg laying and live bearing in elasmobranch fishes. (*a*) Overall numbers of transitions with various forms of live bearing combined. (*b*) As in (*a*), calculated as per-node probabilities of change between states. (*c*) Live bearing divided into yolk only (no nutrient input after fertilization) and subsequent maternal input (matrotrophy). (*d*) As in (*b*), calculated as per-node probabilities of change between states. From Dulvy & Reynolds (1997).

Table 2. Incidence and evolutionary origins of live bearing in vertebrates.

(Birds, turtles and crocodilians are not included because live bearing is not known to occur in any of these taxa. Data for percentages of live bearers are based on taxonomic levels indicated for each column heading. Percentage of elasmobranch live bearers were extrapolated from 350 out of approximately 815 known species.)

	elasmobranch fishes 815 species	teleost fishes species	anurans 315 genera	mammals 1117 genera	squamate reptiles species
% live bearers	60	2–3	< 1	> 99	20
transitions to live bearing	9–10	12	1	2	102–115
transitions from live bearing	1–2	0–1	0	0	?
transitions to maternal input	4–5	4	0	2	3
transitions from maternal input	7–9	0	0	0	0
references[a]	1	2, 3	4	5	6, 7, 8, 9, 10

[a] References: 1, Dulvy & Reynolds 1997; 2, Goodwin *et al.* 2002; 3, Wourms 1981; 4, Clutton-Brock 1991; 5, Zeller 1999; 6, Shine 1985*a*; 7, Shine 1985*b*; 8, Shine 1989; 9, Shine & Lee 1999; 10, Blackburn 1999.

transition from female-only to biparental care (0.06, 95% CI 0.03–0.09) is very similar to the probability of transition from biparental to female-only care. Changes in male contributions may have been due to changes in the needs of the young for provisioning by two parents, or changes in costs to males, such as lost mating opportunities, mobility or foraging success when carrying infants (Woodroffe & Vincent 1994).

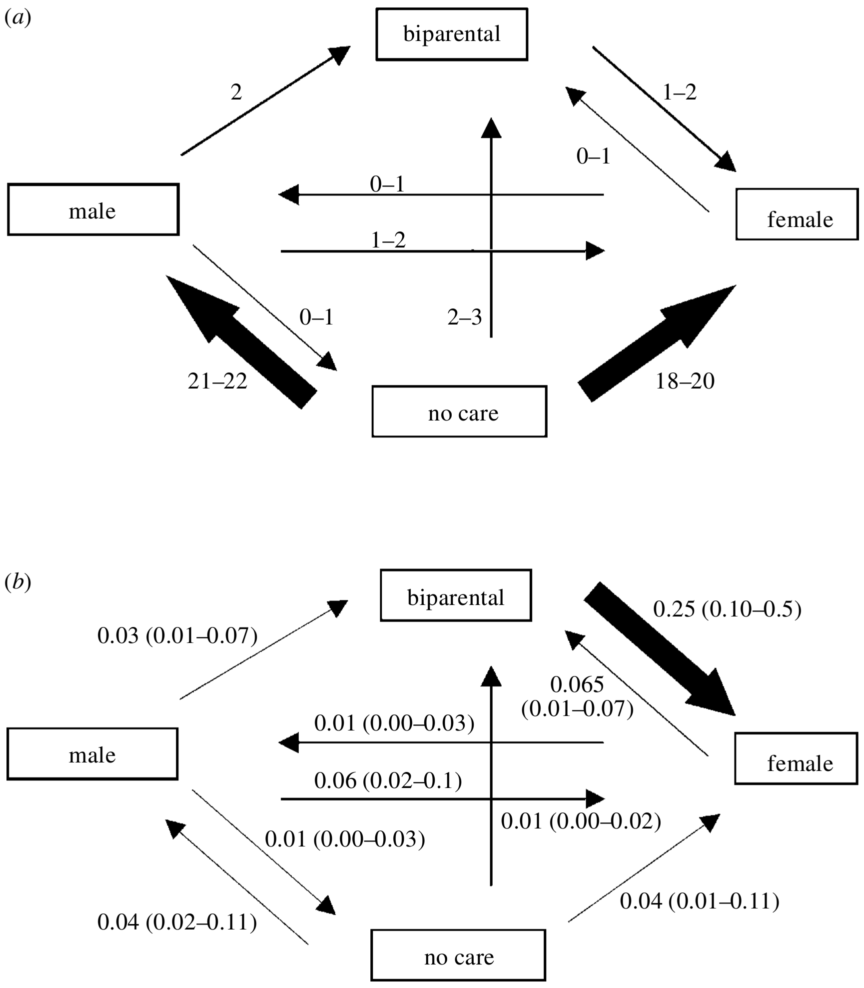

Figure 3. Transitions among four parental care states in frogs and toads (anurans). New analyses based on data from Beck (1998 and unpublished data) and K. Summers (personal communication). (*a*) Total number of changes between states. (*b*) Per-species probabilities of change between states.

(d) *Reptiles*

Most squamate reptiles (snakes and lizards) hide their eggs and do not guard them (Shine 1988) (table 1). However, egg guarding by females occurs in 3% of genera. Biparental care is found in eight species of crocodilians (Greer 1971; Shine 1988; Densmore & White 1991; Aggarwal *et al.* 1994), having evolved two to three times from female care (table 1). Shine & Bull (1979) proposed that egg guarding could be an intermediate step in the evolution of live bearing as taxa adapt to similar environmental conditions by protecting offspring. De Fraipont *et al.* (1996) tested this hypothesis and suggested that egg guarding evolved independently from live bearing. However, this conclusion is tenuous because of the difficulty of detecting female egg guarding in the wild and poorly resolved species relationships (Blackburn 1999; Shine & Lee 1999). Male care is not provided by any squamate reptiles. This may be due to a delay between copulation and egg laying. After copulation, males have time to desert and find additional mates, and females have time to leave the territory or home range of the male.

Live bearing is found in 20% of squamate species (table 2). Reproduction is either via basic egg retention (ovoviviparous) or full live bearing with maternal input (matrotrophy) (Blackburn 1982). Live bearing has been extremely labile in the squamates, having evolved approximately 102–115 times, 31 times alone in the lizard family Scincidae (the skinks) (Blackburn 1999) (table 2). The question of whether there have been reversals back to egg laying is controversial. An analysis by De Fraipont *et al.* (1996) originally overestimated the strength of support for possible reversals to egg laying in snakes and lizards (see Blackburn 1999; Shine & Lee 1999). For a subset of squamates that were analysed by Lee & Shine (1998), parsimony analyses produced evidence for at least 35 transitions to live bearing, and weak evidence for five reversals. Further analyses based on a maximum-likelihood approach do suggest that reversals to egg laying may have evolved in some groups (De Fraipont *et al.* 1999).

(e) *Birds*

(i) *Overall analyses*

There has been controversy about the origins and subsequent transitions in parental care in birds (e.g. Lack 1968; Wesolowski 1994; Ligon 1999). We will not go into detail here, but refer readers to reviews in this issue by Burley & Johnson (2002) and Tullberg *et al.* (2002). Briefly, the argument concerns both pattern and process. We can call the ‘female first’ hypothesis the idea that the oldest birds (Eoaves) had female care, like their presumed ancestors (e.g. Burley & Johnson 2002). Then, a bifurcation is suggested to have occurred, whereby biparental care evolved in the lineage leading to neognaths (modern birds except for palaeognaths: ostriches, rheas, kiwis and tinamous), whereas the lineage leading to palaeognaths adopted exclusive male care (Burley & Johnson 2002).

By contrast, the 'male first' hypothesis is that male care was first (e.g. Van Rhijn 1990; Wesolowski 1994; Ligon 1999). This is possible if ratites and tinamous, and/or buttonquails, are at the base of the avian clade, as some have proposed. If this pattern of male-caring species being basal is correct, the process could be that the males, which are large bodied relative to clutch mass, can care for the offspring of more than one female at a time (e.g. Vehrencamp 2000). Furthermore, females may have been less likely to assume care if this had interfered with egg production. These are very similar arguments to those proposed for fishes, although the ability to care for multiple broods will still be lower in birds.

There have been no phylogenetic analyses for the entire class Aves. However, a recent analysis of the predominant form of incubation among 36 avian clades supported the idea that male care may have been ancestral in birds (Vehrencamp 2000). This analysis was based on a basal placement of ratites (ostriches, rheas and kiwis; see also McKitrick 1992). As the author noted, this placement is tentative, and it has been debated by others (Tullberg *et al.* 2002). Furthermore, the main purpose of the analysis was to examine cooperative breeding in birds, and the taxa were chosen accordingly. Thus, the purpose was different from the one for which we are using the analysis, and it may therefore be biased taxonomically with respect to our questions. The analysis indicates eight independent transitions towards incubation by the female, with all but one transition occurring through biparental intermediaries (table 1). Two transitions to male incubation from shared incubation are also indicated. Although a better understanding of the origins of care in birds may have to await further fossil evidence from avian ancestors, it should also be possible and fruitful to undertake a full phylogenetic analysis of parental care in extant species.

(ii) *Shorebirds*

Shorebirds (part of the infraorder Charadriiformes, excluding gulls and alcids) afford a finer resolution of evolutionary pathways to parental care. They have an unusually high diversity in parental contributions by males and females (Székely & Reynolds 1995). Departure by one sex may occur as soon as the clutch is complete, or during the incubation or brood-rearing phase. Two alternative hypotheses have been suggested about transitions in care. First, as with teleost fishes, it has been proposed that care provided by the male may have been first, followed by the evolution of biparental care and then female care (e.g. Van Rhijn 1990; reviewed by Ligon 1999). One might call this a 'male first' hypothesis. Alternatively, it has also been suggested that biparental care was ancestral within this clade, and evolved subsequently into either male or female care (Jenni 1974; Pitelka *et al.* 1974; Emlen & Oring 1977). We will call this a 'biparental first' hypothesis.

To distinguish between these hypotheses, Székely & Reynolds (1995) traced the sex of the predominant care giver onto a composite phylogeny that included nearly half of the approximately 203 species of shorebirds. This study used a different scoring system for care than the other studies reviewed here because, for example, 'male care' includes species in which the female may also provide some care but abandons the brood before the male does. The study suggested that biparental care may be ancestral, in accordance with the 'biparental first' hypothesis, based on outgroup comparisons (Székely & Reynolds 1995). One can question the various candidates that are considered as potential outgroups to the shorebirds (e.g. Ligon 1999; cf. Burley & Johnson 2002), and this problem awaits better phylogenetic information. The main finding of the study was an ancient transition toward predominantly male care in the Scolopacida (which includes jacanas, snipes, curlews and sandpipers), followed by repeated transitions towards either full biparental care or predominantly female care (table 1). Thus, although a tentative biparental ancestry in shorebirds fits with a 'biparental first' scenario, after the origin of male care in one clade, the numerous transitions back to biparental care fit with the 'male first' scenario.

When the sexes were analysed separately, there was evidence for eight to 14 evolutionary reductions in male care, and only a maximum of two increases. The number of evolutionary reductions by females was similar (9–12), but there have also been 9–12 increases. Thus, the pattern has been for males to reduce their care relative to females, either by deserting broods at some stage prior to fledging, or by being joined by females. This is reminiscent of the pattern proposed for teleost fishes.

We have repeated the analysis of Székely & Reynolds (1995), using the alternative way of classifying care, to make it more comparable with the other studies reviewed here, whereby species are called 'biparental' as long as both sexes make some contribution to the young, regardless of the disparity in their contributions. We have used the most recently available data and phylogenetic evidence for the entire Charadriiformes, thereby including gulls and alcids in addition to shorebirds (Székely *et al.* 2000, T. Székely, personal communication). This analysis paints a slightly different picture, with clearer support for the 'biparental first' scenario, whereby from biparental care there have been several transitions toward both male-only and female-only care (figure 4*a*). The probability of transition from biparental care to male care (0.07) appears to be approximately the same as the probability of transition to female care (0.10). The probabilities of transition to and from female and male care were the same (figure 4*b*).

Attempts to find universal explanations for transitions in the amount of care given by each sex have been only partially successful (Reynolds & Székely 1997). No correlations were found between durations of male or female care and breeding latitudes, hatching success, clutch masses, egg-laying intervals or breeding density. However, taxa with longer durations of male care have shorter migration distances. One might speculate that males cannot meet the dual demands of care and long-distance migration, but it is not clear why females would not also suffer from this trade-off. Further analyses of sex differences in wintering latitude might help to resolve this question. There was a strong correlation between care and sexual size dimorphism, whereby the sex that performed the least care was larger than the opposite sex. This supports the traditional trade-off expected between sexual selection and care, though cause and effect cannot be

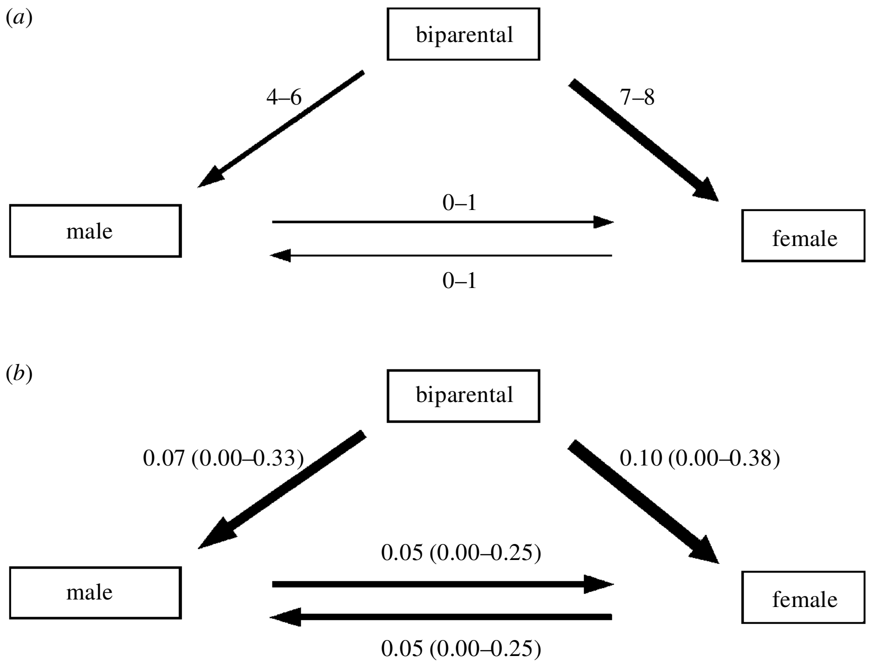

Figure 4. Transitions among the sexes in parental care in shorebirds, gulls and allies (Charadrii). (*a*) New analyses with 'biparental' scored as any contributions by both sexes toward incubation or brood rearing, regardless of disparities in their duration of care (data from Székely *et al.* (2000) and T. Székely (personal communication)). (*b*) As in (*a*), calculated as per-node probabilities of change between states.

distinguished by these analyses. This study reinforced the suggestion that males and females may have evolved care behaviour for different reasons in different taxa (Reynolds 1987).

4. INVERTEBRATES

A treatment of parental care and live bearing in invertebrates warrants a full review of its own. Indeed, live bearing in insects occupied an entire book 50 years ago, with descriptions of various forms of live bearing in 13 insect orders (Hagan 1951). A cursory review of the literature shows that some invertebrate taxa have independently evolved live bearing many times. Dipterans stand out in this regard, with a conservative estimate of 61 origins (Meier *et al.* 1999). This estimate was based on a careful and critical appraisal of the literature, as indicated by a section in Meier *et al.*'s paper entitled 'Dubious reports of viviparity in additional families'. The estimates of transitions were not based on explicit reference to phylogenies, because this information is lacking for many species in the order. However, like Gittleman (1981), the authors' reasoning was similar to outgroup analysis with reference to crude taxonomic information. They did not estimate reversals back to egg laying, because they assumed *a priori* that reversal would be rare. In other words, their reasoning was similar to using ordered character states. This might overestimate transitions to live bearing and underestimate reversals. An overall correlate of live bearing in dipterans appears to be the use of unpredictable or ephemeral substrates for the offspring, but this conclusion awaits formal phylogenetic analyses.

Live bearing is found in many species of echinoderms. For example, a species of sea cucumber is known to retain juveniles internally and feed them nutrition that increases the dry weight from egg to 8 mm juveniles more than 100-fold (Frick 1998). Live bearing has evolved once in a clade of 18 species of deep-sea holasteroids (Mooi & David 1996) and twice in 12 species of asterinid starfishes (Hart *et al.* 1997). Various species of unionid mussels also retain juveniles, and there is evidence for a single transition to this form of live bearing in a clade of 21 species of oyster (Ó Foighil & Taylor 2000). Other marine taxa that brood their young include ophiuroids, chitons, slipper limpets and octopuses (see references in Strathmann & Strathmann (1982)).

Parental care is rare in terrestrial arthropods, and this is most often performed by the female alone, followed by biparental and then male care (Zeh & Smith 1985). Care appears to be associated with environments that are harsh or that contain strong predation pressures (Clutton-Brock 1991). Various forms of care have clearly evolved on numerous occasions, judging by the disparate taxonomic distribution of care among groups such as spiders, mites, woodlice, centipedes, millipedes and insects. However, considering the huge number of species of such arthropods, evolutionary transitions to care have remained proportionately extremely rare.

Exclusive paternal care is thought to have evolved at least eight times in arthropods (reviewed by Tallamy (2000)). In the marine environment, paternal care by invertebrates is rare, with the best-known example being sea spiders (pycnogonids), in which males carry the offspring in seven out of the eight families (King 1973). Tallamy (2000) has assembled evidence that paternal care in arthropods may have evolved due to enhanced sexual selection on males, through female preferences for males that are guarding eggs.

5. GENERAL DISCUSSION

(a) *Limits to inferences*

Phylogenies are hypotheses about evolutionary relationships. At best, the studies reviewed here have been pieced together from various kinds of molecular and non-molecular data that differ in quality (e.g. cichlids, elasmobranchs, shorebirds and anurans). At worst, there were no group-wide phylogenies at all, and the inferences were based on best guesses from crude taxonomic information (e.g. teleost fishes and dipterans). However, in the studies that we have been directly involved in (cichlids, shorebirds and elasmobranchs), we have found that the overall results have been robust against various alternative phylogenies that have been proposed. Thus, although the numbers of transitions will undoubtedly change as more information becomes available, we believe that the overall directions of transitions are probably correct. This kind of uncertainty is not unique to phylogenetic information; there are errors around all statistical estimates, including those derived from experimental studies.

There are limitations in the techniques for reconstruction. The analyses reported here are based on parsimony, whereby ancestral character states are estimated by minimizing the total number of changes over all branches of the tree (Maddison & Maddison 1992). This method has several assumptions, such as that changes are distributed randomly over the tree, and that transitions are rare (Martins & Hansen 1996; Martins 2000). When transitions are common, ancestral reconstructions are less certain, especially when distant ancestors are involved (Schluter *et al.* 1997; Martins 2000). This is ironic, because many of the studies that we have reviewed here were carried out precisely because transitions were expected to be common. Thus, although parsimony might seem to involve minimal assumptions about the pattern of evolutionary change, in fact its assumption of rare change involves an underlying view of the way in which evolution works, which may not fit with many of the adaptive scenarios that are being tested.

Maximum likelihood can be used to assess the accuracy of ancestral reconstructions (Schluter *et al.* 1997). Here, too, some sort of underlying model of change is specified, such as a random walk through time, represented by a Markov process (Pagel 1994). Other underlying models can be used, if there are grounds for thinking that they apply. Ideally, branch lengths should be incorporated into the analyses, though these are often unavailable, especially for trees such as those reviewed here, which are often based on non-molecular data. It is prudent to be cautious in interpreting transitions between distant relatives, especially if transitions have been common in the tree.

We presented two methods for measuring evolutionary change. These differ in the way that they account for variations in ages and distributions of character states. Simple counts of inferred transitions measure the number of nodes that have changed on the tree, but do not account for the frequency with which characters occur. Our analyses of transition rates overcome this problem and they have an intuitive interpretation: for instance, to ask how many times female care has evolved from biparental care as opposed to male care, we should consider how much of the tree consists of biparental care or male care, as well as the ages of these branches. If a tree is dominated by ancient biparental care, female care will be expected to evolve more often from biparental care than from male care.

(b) *Overall patterns*

We began this review by presenting the four potential contributions towards care by males, females, both sexes or neither as a series of potential transitions between pairs of character states (figure 1). Few of the taxonomic groups that we have considered contain all four of these states, and some might argue that the inclusion of live bearing muddies the waters, though the benefits and many of the costs of live bearing are similar to those proposed for care (e.g. Clutton-Brock 1991). Thus, we have mapped the dominant transitions shown by each group onto a single diagram, to try to pick out common themes across taxa (figure 5). This has not been easy! Transitions from no care to male care have occurred primarily in teleost fishes and anurans, although as a percentage per lineage this has been rare (figure 5*b*). We have also seen several cases in arthropods (Tallamy 2000), and this transition has also been suggested for early birds (reviewed by Ligon (1999)). It is tempting to search for a common explanation for the prevalence of this transition in these taxa. We propose that most of these cases can be explained by male territoriality and low costs of care per offspring. This could lead to the evolution of male care as a form of sexual selection, except in courtship-role-reversed species. It is interesting to note that many of the papers reviewed above have also made this suggestion for their particular taxonomic groups, although few have crossed taxonomic lines in seeking a general explanation (but see Tallamy (2000)). It would be helpful if empirical studies could be performed on a wider range of taxa to examine the costs and benefits through sexual selection of providing care. Note that we have not found evidence for any taxon having evolved in the other direction, i.e. from male care to no care. Studies that manipulate male care might be able to tell us whether this transition is hampered by costs to the young or by costs to the male's mating success.

To date, the taxon that shows the most transitions from male to biparental care is the shorebirds, when care is scored according to predominant sex of the care giver (e.g. Székely & Reynolds 1995; table 1). However, there is also good evidence for shorebirds and allies having evolved in the opposite direction when care is scored as biparental and there are any joint efforts by males and females in incubation or brood rearing, and the terms 'male care' and 'female care' are reserved only for cases in which all of the care is provided by one sex (figure 4). It would be nice to be able to complement this study with studies of other taxa in which the extent of care can be scored, rather than pooling disparate contributions by each sex into a single category as 'biparental'.

Biparental to female care transitions are well supported by cichlid fishes, shorebirds and probably by many additional bird species, although general statements about birds await broader taxonomic comparisons. Primates, by contrast, have often evolved in the opposite direction. As discussed in the taxonomic section, and shown by our new analyses of transition probabilities, this is not surprising, given the prevalence of female care deep in the tree.

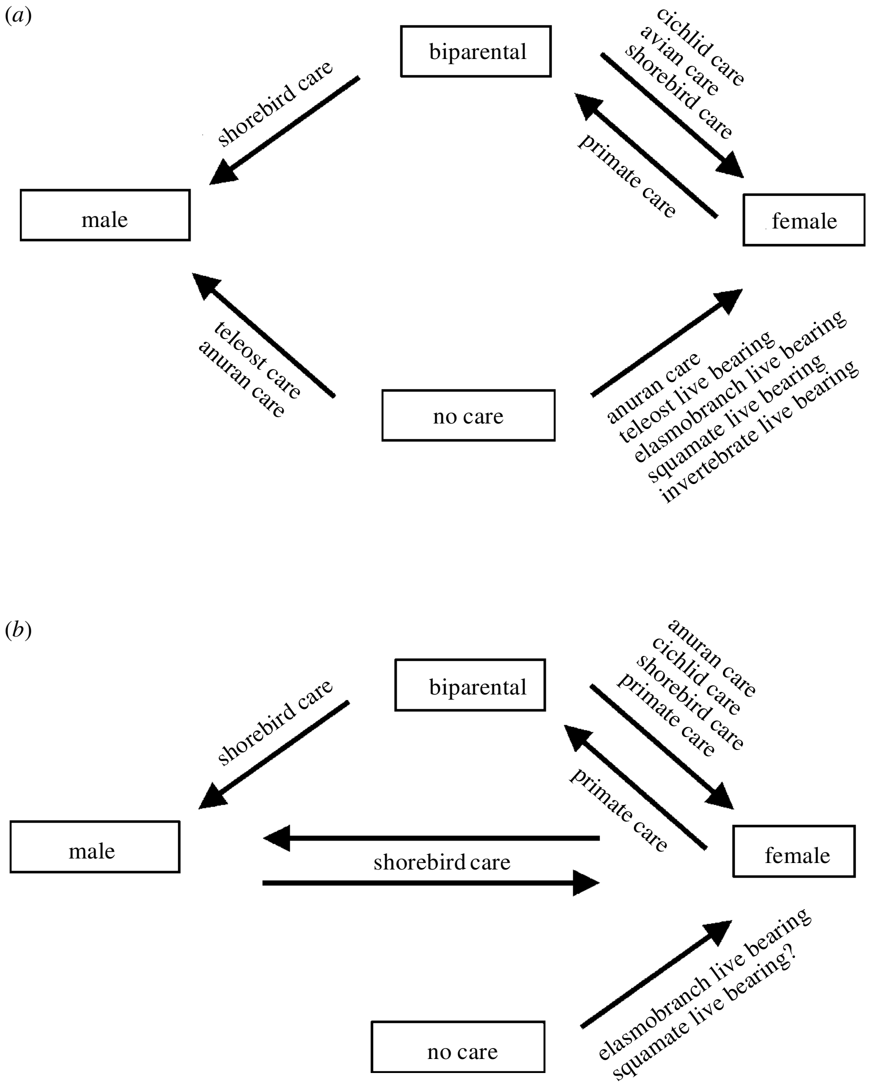

Figure 5. Dominant directions of change in male and female parental contributions to offspring, including care and live bearing. The strength of evidence for each pattern is discussed in the text, but note that evidence for transitions involving birds and teleost fishes is preliminary and awaits formal overall analyses. (*a*) Number of transitions; (*b*) probability of transitions per node.

The transitions between no care and female care (including live bearing) show a symmetry to those between no care and male care, with all transitions being away from no care and showing few reversals (figure 5, table 1). Thus, anuran care, as well as live bearing in teleosts, elasmobranchs, squamate reptiles and invertebrates have all undergone numerous transitions toward female inputs to the young from a state of no care and egg laying. As discussed earlier, explanations of where traits have come from require consideration of the prevalence and age of the ancestral states, and it is not surprising that live bearing would be derived from egg laying more often than vice versa, given the prevalence of egg laying in these taxa.

We have no desire to squeeze taxa into patterns in which they do not fit comfortably, and although we have focused on dominant patterns of transitions, it is also worth considering reversals in some detail. There is evidence for reversals in both parental care and parity in most of the taxa examined. The smaller number of reversals from live bearing to egg laying has been interpreted with respect to Dollo's law (Dollo 1893), which suggests in its broadest form that evolution is irreversible (cf. Teotónio & Rose 2000). More narrowly, the law dictates that once complex organs have been lost, they are unlikely to be regained in the same form, especially with the same genetic basis. Evidence that appears to support the broad form of the Dollo's law can be found in the rarity of reversals in four studies: elasmobranch fishes (Dulvy & Reynolds 1997), teleost fishes (Goodwin *et al.* 2002), squamate reptiles (Lee & Shine 1998) and polychaete worms (Rouse & Fitzhugh 1994).

Although the patterns of transitions in parity fit with the Dollo's law, is this a result of the process envisaged by Dollo? We are sceptical, for three reasons. First, as Lee & Shine (1998) noted, it is not clear that a transition from egg laying to live bearing involves mainly the loss of complex structures, because live bearing is arguably just as 'complex' as egg laying, given the numerous structural and behavioural adaptations that it entails. If live bearing is more 'complex', we are outside the law's jurisdiction, at least in the law's narrow form. Second, among reptiles, some squamates undergo advanced embryonic development inside the female and may therefore have a much 'easier' time taking the final step toward live bearing than others, such as turtles, crocodilians and tuataras (Andrews & Mathies 2000). Indeed, several species of squamate are facultative live bearers. Thus, it is not difficult to imagine that if there were changes in selection pressure, these might also readily cause a reversal to egg laying. The failure to evolve such reversals may not be due to a law-abiding nature, but instead due to lack of selection. Third, by definition, there will be less time for a reversal than for the initial evolution of a trait. Therefore, Dollo's law should be tested against a null hypothesis that accounts for time, to enable comparable estimates of transition probabilities.

In conclusion, this review indicates that many taxa show consistent trends in the evolution of care, such as reductions in the amount of care provided by males relative to females (shorebirds and cichlid fishes) or the reverse (teleost fishes overall and primates). However, other taxa, such as frogs and toads, as well as shorebirds (depending on how care is scored), cannot be placed into either of these trends, with both sexes equally likely to increase (anurans) or decrease (shorebirds) their care. There is considerable room for improvement in many of the assessments reviewed here, especially in terms of phylogenetic information and methods of inference. However, the new analyses that we provide concerning transition probabilities represent an advance over previous analyses that examined transition counts without accounting for prevalence of each character state. As we improve our understanding of the directions of change in care and live bearing, we will be in a better position to test adaptive hypotheses to explain the diversity of contributions by each sex.

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REFERENCES

Aggarwal, R. K., Majumdar, K. C., Land, J. W. & Singh, L. 1994 Generic affinities among crocodilians as revealed by DNA fingerprinting with a Bkm-derived probe. *Proc. Natl Acad. Sci. USA* **91**, 10 601–10 605.

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Andrews, G. M. & Mathies, T. 2000 Natural history of reptilian development: constraints on the evolution of viviparity. *BioScience* **50**, 227–238.

Balshine-Earn, S. & Earn, D. J. D. 1998 On the evolutionary pathway of parental care in mouth-brooding cichlid fish. *Proc. R. Soc. Lond.* B **265**, 2217–2222. (DOI 10.1098/rspb.1998.0562.)

Barlow, G. W. 1974 Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeon fishes. *Am. Zool.* **14**, 9–34.

Baylis, J. R. 1981 The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. *Environ. Biol. Fishes* **6**, 223–251.

Beck, C. W. 1998 Mode of fertilization and parental care in anurans. *Anim. Behav.* **55**, 439–449.

Blackburn, D. G. 1982 Evolutionary origins of viviparity in the Reptilia. I. Sauria. Amphibia. *Amphibian Reptilia* **3**, 185–205.

Blackburn, D. G. 1992 Convergent evolution of viviparity, matrotrophy, and specialisations 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.

Blumer, L. S. 1979 Male parental care in the bony fishes. *Q. Rev. Biol.* **54**, 149–161.

Burley, N. T. & Johnson, K. 2002 The evolution of avian parental care. *Phil. Trans. R. Soc.* B **357**, 241–250. (DOI 10.1098/rstb.2001.0923.)

Clough, M. & Summers, K. 2000 Phylogenetic systematics and biogeography of the poison frogs: evidence from mitochondrial DNA sequences. *Biol. J. Linn. Soc.* **70**, 515–540.

Clutton-Brock, T. H. 1991 *The evolution of parental care*. 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.

De Fraipont, M., Clobert, J., Meylan, S. & Barbault, R. 1999 On the evolution of viviparity and egg-guarding in squamate reptiles: a reply to R. Shine and M. S. Y. Lee. *Herpetologica* **55**, 550–555.

Densmore III, L. D. & White, P. S. 1991 The systematics and evolution of the Crocodilia as suggested by restriction endonuclease analysis of mitochondrial and nuclear ribosomal DNA. *Copeia* **1991**, 602–615.

Dewsbury, D. A. 1985 Paternal behaviour in rodents. *Am. Zool.* **25**, 841–852.

Dollo, L. 1893 Les lois de l'évolution. *Bull. Soc. Belge Géol. Pal. Hydr.* **7**, 164–166.

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.)

Emlen, S. T. & Oring, L. W. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.

Frick, J. E. 1998 Evidence of matrotrophy in the viviparous holothuroid echinoderm *Synaptula hydriformis*. *Invert. Biol.* **117**, 169–179.

Gittleman, J. L. 1981 The phylogeny of parental care in fishes. *Anim. Behav.* **29**, 936–941.

Goodwin, N. B., Balshine-Earn, S. & Reynolds, J. D. 1998 Evolutionary transitions in parental care in cichlid fishes. *Proc. R. Soc. Lond.* B **265**, 2265–2272. (DOI 10.1098/rspb.1998.0569.)

Goodwin, N. B., Dulvy, N. K. & Reynolds, J. D. 2002 Life-history correlates of the evolution of live bearing in fishes. *Phil. Trans. R. Soc. Lond.* B **357**, 259–267. (DOI 10.1098/rstb.2001.0958.)

Grafen, A. & Ridley, M. 1996 Statistical tests for discrete cross-species data. *J. Theor. Biol.* **193**, 255–267.

Greer, A. E. 1971 Crocodilian nesting habits and evolution. *Fauna* **2**, 20–28.

Gross, M. R. & Sargent, R. C. 1985 The evolution of male and female parental care in fishes. *Am. Zool.* **25**, 807–822.

Hagan, H. R. 1951 *Embryology of the viviparous insects*. New York: Ronald Press.

Hart, M. W., Byner, M. & Smith, M. J. 1997 Molecular phylogenetic analysis of life-history evolution in asterinid starfish. *Evolution* **51**, 1848–1861.

Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.

Jenni, D. A. 1974 Evolution of polyandry in birds. *Am. Zool.* **14**, 129–144.

Keenleyside, M. H. A. 1983 Mate desertion in relation to adult sex-ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Anim. Behav.* **31**, 683–688.

Keenleyside, M. H. A. 1991 *Cichlid fishes: behaviour, ecology and evolution*. London: Chapman & Hall.

King, P. E. 1973 *Pycnogonids*. London: Hutchinson & Co.

Kleiman, D. G. & Malcolm, J. R. 1981 The evolution of male parental investment in mammals. In *Parental care in mammals* (ed. D. J. Gubernick & P. H. Klopfer), pp. 347–387. New York: Plenum.

Lack, D. 1968 *Ecological adaptations for breeding in birds*. London: Methuen.

Lee, M. S. Y. & Shine, R. 1998 Reptilian viviparity and Dollo's law. *Evolution* **52**, 1441–1450.

Ligon, J. D. 1999 *The evolution of avian breeding systems*. Oxford University Press.

Low, B. S. 1978 Environmental uncertainty and the parental strategies of marsupials. *Am. Nat.* **112**, 197–218.

Lund, R. 1980 Viviparity and intrauterine feeding in a new holocephalan fish from the lower carboniferous of Montana. *Science* **209**, 697–699.

McKitrick, M. C. 1992 Phylogenetic analysis of avian parental care. *Auk* **109**, 828–846.

Maddison, W. P. & Maddison, D. R. 1992 *MacClade: analysis of phylogeny and character evolution*, v. 3. 0. Sunderland, MA: Sinauer Associates.

Martins, E. P. 2000 Adaptation and the comparative method. *Trends Ecol. Evol.* **15**, 296–299.

Martins, E. P. & Hansen, T. F. 1996 The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. In *Phylogenies and the comparative method in animal behavior* (ed. E. P. Martins), pp. 22–75. Oxford University Press.

Meier, R., Kotrba, M. & Ferrar, P. 1999 Ovoviviparity and viviparity in the Diptera. *Biol. Rev.* **74**, 199–258.

Mooi, R. & David, B. 1996 Phylogenetic analysis of extreme morphologies: deep-sea holasteroid echinoids. *J. Nat. Hist.* **30**, 913–953.

Nussbaum, R. A. & Schultz, D. L. 1989 Coevolution of parental care and egg size. *Am. Nat.* **133**, 591–603.

Ó Foighil, D. & Taylor, D. J. 2000 Evolution of parental care and ovulation behaviour in oysters. *Mol. Phylog. Evol.* **15**, 301–313.

Pagel, M. 1994 Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond.* B **255**, 37–45.

Parker, G. A., Royle, N. J. & Hartley, I. R. 2002 Intrafamilial conflict and parental investment: a synthesis. *Phil. Trans. R. Soc. Lond.* B **357**, 295–307. (DOI 10.1098/rstb.2001.0950.)

Pitelka, F. A., Holmes, R. T. & Maclean Jr, S. F. 1974 Ecology and evolution of social organization in Arctic sandpipers. *Am. Zool.* **14**, 185–204.

Purvis, A. 1995 A composite estimate of primate phylogeny. *Phil. Trans. R. Soc. Lond.* B **348**, 405–421.

Reynolds, J. D. 1987 Mating system and nesting biology of the red-necked phalarope *Phalaropus lobatus*: what constrains polyandry? *Ibis* **129**, 225–242.

Reynolds, J. D. 1996 Animal breeding systems. *Trends Ecol. Evol.* **11**, 68–72.

Reynolds, J. D. & Jones, J. C. 1999 Female preference for preferred males is reversed under low oxygen conditions in the common goby (*Pomatoschistus microps*). *Behav. Ecol.* **10**, 149–154.

Reynolds, J. D. & Székely, T. 1997 The evolution of parental care in shorebirds: life histories, ecology and sexual selection. *Behav. Ecol.* **8**, 126–134.

Rouse, G. & Fitzhugh, K. 1994 Broadcasting fables: is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. *Zool. Scr.* **23**, 271–312.

Sargent, R. C. 1997 Parental care. In *Behavioural ecology of teleost fishes* (ed. J.-G. Godin), pp. 292–315. Oxford University Press.

Sargent, R. C. & Gross, M. R. 1993 Williams' principle: an explanation of parental care in teleost fishes. In *Behaviour of teleost fishes* (ed. T. J. Pitcher), pp. 275–293. London: Chapman & Hall.

Schluter, D., Price, T., Mooers, A. O. & Ludwig, D. 1997 Likelihood of ancestor states in adaptive radiation. *Evolution* **51**, 1699–1711.

Sheldon, B. C. 2002 Relating paternity to parental care. *Phil. Trans. R. Soc. Lond.* B **357**, 341–350. (DOI 10.1098/rstb.2001.0931.)

Shine, R. 1985*a* The evolution of viviparity in reptiles: an ecological analysis. In *Biology of the reptilia*, vol. 15 (ed. C. Gans & F. Billet), pp. 605–694. New York: Wiley.

Shine, R. 1985*b* The evolution of viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. *Oecologia* **57**, 397–405.

Shine, R. 1988 Parental care in reptiles. In *Biology of the reptilia* (ed. C. Gans & R. B. Huey), pp. 276–329. New York: A. R. Liss.

Shine, R. 1989 Ecological influences on the evolution of vertebrate viviparity. In *Complex organismal functions: integration and evolution in vertebrates* (ed. G. Roth & M. H. Wake). London: Wiley.

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.

Strathmann, R. R. & Strathmann, M. F. 1982 The relationship between adult size and brooding in marine invertebrates. *Am. Nat.* **119**, 91–101.

Székely, T. & Reynolds, J. D. 1995 Evolutionary transitions in parental care in shorebirds. *Proc. R. Soc. Lond.* B **262**, 57–64.

Székely, T., Webb, J. N., Houston, A. I. & McNamara, J. M. 1996 An evolutionary approach to offspring desertion in birds. *Curr. Ornithol.* **13**, 271–330.

Székely, T., Reynolds, J. D. & Figuerola, J. 2000 Sexual size dimorphism in shorebirds, gulls and alcids: the influence of sexual and natural selection. *Evolution* **54**, 1404–1413.

Tallamy, D. W. 2000 Sexual selection and the evolution of exclusive paternal care in arthropods. *Anim. Behav.* **60**, 559–567.

Teotónio, H. & Rose, M. R. 2000 Variation in the reversibility of evolution. *Nature* **408**, 463–466.

Tullberg, B., Ah-King, M. & Temrin, H. 2002 Phylogenetic reconstruction of parental-care systems in the ancestors of birds. *Phil. Trans. R. Soc.* B **357**, 251–257. (DOI 10.1098/rstb.2001.0932.)

Van Rhijn, J. G. 1990 Unidirectionality in the phylogeny of social organization, with special reference to birds. *Behaviour* **115**, 153–174.

Vehrencamp, S. L. 2000 Evolutionary routes to joint-female nesting in birds. *Behav. Ecol.* **11**, 334–344.

Wesolowski, T. 1994 On the origin of parental care and the early evolution of male and female parental roles in birds. *Am. Nat.* **143**, 39–58.

Wilkinson, M. & Nussbaum, R. A. 1998 Caecilian viviparity and amniote origins. *J. Nat. Hist.* **32**, 1403–1409.

Williams, G. C. 1975 *Sex and evolution*. Princeton University Press.

Woodroffe, R. & Vincent, A. 1994 Mother's little helpers: patterns of male care in mammals. *Trends Ecol. Evol.* **9**, 294–297.

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. Fishes* **21**, 473–515.

Zeh, D. W. & Smith, R. L. 1985 Paternal investment by terrestrial arthropods. *Am. Zool.* **25**, 785–805.

Zeller, U. 1999 Mammalian reproduction: origin and evolutionary transformations. *Zool. Anz.* **238**, 117–130.